MOVEMENT AND SPACE-USE AMONG BORNEAN ORANGUTANS

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to The Housemates

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Summary

The movement and space-use of an animal is a fundamental aspect of its ecology. How, where, and when an animal moves through its habitat is influenced by a complex web of individual, internal, and external factors. The overarching aim of this dissertation is to gain a better understanding of the factors that influence and shape orangutans' movement and space-use. A secondary aim of this dissertation is to specifically investigate the influence of fruit availability on orangutans' ranging patterns, with a focus on adult females. The studies compiled here shed light on orangutan movement, substrate use, and home ranging patterns over different temporal and spatial scales. Specifically, I investigate ground-use among orangutans, female home ranges establishment, and female orangutan ranging responses to preferred resource scarcity.

Analyses are based on data collected on two populations of wild orangutans in Indonesia: Tuanan in Central Kalimantan (*P. p. wurmbii*), and Wehea in East Kalimantan (*P. p. morio*). The Tuanan study area is composed of homogeneous, formerly selectively-logged, peat-swamp forest, which, under normal conditions, experiences within-year seasonal fluctuations in fruit availability that are relatively predictable, with only short periods of low fruit availability. In contrast, the Wehea region consists predominantly of relatively undisturbed lowland dipterocarp forest, which experiences extreme long-term fruit scarcity, punctuated by marked supra-annual masting events.

In Chapter 1, I identify the major causes of terrestriality among the Tuanan orangutan population. Orangutans spent, on average, 2.29% of the total observation time on the ground. I show that orangutans descend to the ground to acquire and consume water and food resources (especially insects), to travel, and to evade conspecifics. Terrestrial travel may be an energy-efficient means of locomotion, especially for flanged male orangutans (the largest bodied age-sex class). Thus, ground-use is not simply a response to canopy gaps and/or forest fragmentation and the need to cross open areas, as has been suggested, but rather is a natural part of orangutans' behavioral repertoire.

In Chapter 2, I aim to better understand *how* and *where* young female Bornean orangutans establish their home ranges. I use detailed longitudinal data of four young female orangutans at Tuanan to trace changes in their socio-spatial patterns as they matured from dependent offspring to primiparous adult females. I show that young females go through an 'exploration phase,' beginning when they are independent immatures and lasting through their adolescence, characterized by an increase in home range size and distance travelled each day. This exploration is facilitated by high resource availability and association with adult males. Young females settle into home ranges that overlap with their mothers' and other maternal relatives' after the birth of their first offspring, and maintain preferential association with their mothers throughout this entire process. Our findings indicate that the high habitat productivity and high orangutan population density of Tuanan lead to a high degree of life-time site-fidelity and overlap among maternal kin.

In Chapter 3, I identify variation in ecological strategies used to cope with resource scarcity among orangutans, and specifically investigate the criteria that lead to a ranging response, rather than a dietary response, to scarcity. I compare the influence of fruit scarcity on the ranging patterns of female Bornean orangutans living under two different long-term ecological conditions: 1) relatively stable, predictable seasonal fluctuations in fruit availability

with widespread high-quality fallback foods at the Tuanan site, and 2) long periods of extreme fruit scarcity with occasional supra-annual masts at the Wehea site. I show that female orangutans living in these two habitats exhibit different responses to scarcity: females at Tuanan engage in diet switching and shrink their home ranges, whereas females at Wehea move over long distances, likely area-switching. I conclude that female orangutans at Wehea employ this ranging response because of the duration and severity of resource scarcity at this site, and that this response may be facilitated by the fine spatial grain of the habitat and their propensity for energetically low-cost ground travel, and further enabled by the low population density which allows for females to move unimpeded through the habitat without risk of agonistic encounters. At Tuanan, on the other hand, the existence of decent-quality ubiquitous fallback foods enables diet-switching, while the high population density may increase the risk of social aggression that wide-ranging females would incur, thus further discouraging area-switching in response to scarcity.

These results provide a better understanding of several of the factors affecting movement and space-use among orangutans. In particular, my results increase our understanding of the conditions that favor a ranging versus a dietary response to scarcity of preferred foods, and show how population density may influence female orangutan ranging patterns and transgenerational site-fidelity. These results have important implications for orangutan conservation, and should be considered when designing and implementing landscape planning and translocation initiatives.

General Introduction and Discussion

INTRODUCTION

The movement and space-use of an animal is a fundamental aspect of its ecology. How, where, and when an animal moves through its habitat is influenced by a complex web of individual, internal, and external factors. This dissertation explores movement, substrate-use, and home ranging patterns among wild Bornean orangutans (*Pongo pygmaeus subspp.*) over different temporal and spatial scales. Analyses are based on data collected on two populations of wild orangutans in Indonesia. The results provide a better understanding of several of the factors affecting movement and space-use among orangutans, and have implications for orangutan ecology, culture, and conservation.

Background

Movement and home ranges

How, where, and when an animal moves is the result of a complex interplay between its own individual characteristics and internal state, and external biotic and abiotic factors in its environment (Börger et al. 2008). Many factors, and the interactions between them, can affect how and where an animal moves: age-sex class (Messier 1985; Bates and Byrne 2009), body size (Blouin-Demers et al. 2007), reproductive status (Singh and Ericsson 2014), social and dominance relationships with conspecifics (Höjesjö et al. 2007), physiological state (Jachowski and Singh 2015), the spatial and temporal distribution of plant resources (Edwards et al. 2013; Merkle et al. 2016), water sources (Scholz and Kappeler 2004), and prey and/or predators (Willems and Hill 2009; Kittle et al. 2016; Pokallus and Pauli 2016), the location and movement of conspecifics (Strandburg-Peshkin et al. 2015), and temperature/climate (Stelzner 1988). In turn, an animal's movement directly and indirectly affects these factors, creating a feedback loop between movement decisions and the factors that influence them (Börger et al. 2008). This interplay occurs over different temporal and spatial scales – from micro-level choices of substrate and travel direction for each single movement step, to macro-level patterns such as a long-distance migration or bounded home ranging.

On a micro level, movement can be broken up into single steps, based on time elapsed or distance and direction travelled. For arboreal animals, movement steps are as much about *how* to move as they are about *where* to move. Indeed, arboreal mammals have been shown to exhibit higher locomotor diversity than terrestrial mammals – using a more diverse repertoire of locomotor and positional behaviors to navigate the complex 3-dimensional habitat of a forest canopy (Granatosky 2018). Additionally, terrestrial movement has been observed across a range of habitually-arboreal primate taxa, for the purposes of accessing particular feeding trees (Shanee and Shanee 2011), obtaining ground-based food and water sources (Souza-Alves et al. 2019), escaping aggressive interactions with conspecifics (Campbell et al. 2005), and moving and foraging through heavily disturbed habitats and between forest fragments (Riley 2008; Martínez and Wallace 2011). This flexibility with regards to primate locomotion and substrate-use is just one example of the ways in which the factors affecting animal movement play out on a micro, local scale.

On a macro level, most animals exhibit some degree of site-fidelity, meaning that the sum of their movement patterns – given enough time – take on a bounded form. Burt (1943) defined an animal's home range as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young," and he explicitly excluded "occasional sallies outside the area, perhaps exploratory in nature" (p. 351). This definition underlies the study and quantification of animal home ranges, though increasingly more emphasis is placed on explicitly recognizing temporal changes in animal space-use (Fieberg and Börger 2012). Putting more emphasis on the animal's (rather than the researcher's) point of view, Powell and Mitchell (2012) defined a home range as "that part of an animal's cognitive map that it chooses to keep up-to-date with the status of resources… and where it is willing to go to meet its requirements" (p. 953). This definition highlights one of the primary benefits of bounded movement and site-fidelity: familiarity with one's surroundings, including the spatial and temporal distributions of important resources (food, nest sites, escape routes from predators, etc) (Powell 2000).

Natal philopatry and dispersal

Natal dispersal is defined as the permanent movement from the natal area or group (i.e. the area or social group in which an animal was born) to the breeding area or group (i.e. the area or group in which the animal will spend at least part of its adult/reproductive phase) (Greenwood 1980; Johnson and Gaines 1990). Natal philopatry, on the other hand, is the continued residence – even after reaching sexual maturity – of an animal in its natal area or group (Greenwood 1980; Waser and Jones 1983). For group-living animals, philopatry and dispersal are often defined in terms of group residence, or a distinction between locational and social philopatry/dispersal can be made (Isbell and Van Vuren 1996). For predominantly solitary animals, however, philopatry and dispersal are usually defined in terms of location only (Waser and Jones 1983).

Across animal taxa, it is common that patterns of philopatry and dispersal are sex-biased, with one sex generally remaining philopatric to the natal group/area, while the other sex disperses (Greenwood 1980). The ultimate causes of dispersal, and the reasons why it is beneficial for at least one of the sexes to disperse, include inbreeding avoidance, reduced competition between kin, and the potential to negotiate spatial and temporal access to resource patches (Johnson 1986; Bowler and Benton 1999). The costs of dispersal, on the other hand, and the reasons why it may be beneficial for at least one of the sexes to be philopatric, include energetic costs (of dispersal movement to the new area), time costs (due to reduced investment in other activities while dispersing), risk costs (exposure to predators or hostile conspecifics during or after dispersal), and opportunity costs (the loss of potential advantages that would be gained by not dispersing, e.g. social bonds with same-sex kin) (Bonte et al. 2011).

Which sex disperses and which remains philopatric is a question of the costs and benefits to both sexes of adopting either strategy (Greenwood 1980). There is some evidence that the sex for whom the costs of dispersing have the least negative effect on individuals' survival and reproductive success will be the one which disperses (Johnson 1986; Johnson and Gaines 1990). This suggests that, generally, it is always advantageous to be philopatric and the sex that remains philopatric in any given animal population is that which would suffer the higher fitness costs from dispersing. The majority of mammal species exhibit female philopatry with male-biased dispersal (Greenwood 1980). The direction of a sex bias in dispersal has a direct effect on spatial gene flow, and thus on a population's structure and dynamics (Bowler and Benton 1999; Bonte et al. 2011).

Responses to scarcity

Scarcity is defined as the reduced availability of preferred resources usually lasting several months (van Schaik and Brockman 2005). Scarcity exerts strong selective pressure, and thus animals living in seasonal, unpredictable, or harsh habitats exhibit particular adaptations that mitigate the fitness costs induced by scarcity. Common examples of such adaptations among primates include faster life histories (Knott 2009), smaller brain sizes (the expensive tissue hypothesis; Isler and van Schaik 2009) or larger brain sizes (the cognitive buffer hypothesis; Allman 2000; Sol 2008) (see also van Woerden et al. 2010; van Woerden et al. 2011; van Woerden et al. 2014), specialized morphologies to digest or process fallback foods (Marshall and Wrangham 2007; Marshall et al. 2009a), seasonal reproduction (Brockman and van Schaik 2005), and heterothermy (Dausmann 2014; Ruf and Geiser 2014). Interwoven with such adaptations are more general scarcity-coping adaptations: evolved physiological and/or behavioral plasticity, i.e. the ability to respond flexibly to changes in one's habitat.

Among primate taxa that exhibit behavioral and physiological plasticity, animals are able to employ various ecological strategies in order to survive when their preferred resources are scarce (van Schaik et al. 1993). These strategies include physiological responses such as storing fat during periods of abundance and metabolizing these fat stores during periods of scarcity (Knott 1998), relaxing thermoregulatory control during sleep (Berger and Phillips 1995), temporarily suspending reproduction (Brockman and van Schaik 2005), and – among heterotherms - manipulating the occurrence, timing, duration, and/or depth of torpor (Schmid and Speakman 2000; Giroud et al. 2008; Nowack et al. 2010; Canale et al. 2011). Ecological strategies to cope with scarcity often also include behavioral responses such as altering the daily activity budget (Ganzhorn et al. 2003) and/or activity patterns (Erkert and Kappeler 2004), increasing (Vedder 1984) or decreasing (Zhang 1995) daily travel distance , expanding, contracting, or shifting one's home range (Mitani 1989; Li et al. 2000; Scholz and Kappeler 2004), increasing reliance on lower quality, ubiquitous, fallback foods (Grueter et al. 2009) and/or foods requiring extractive foraging techniques (Yamakoshi 1998), and – among taxa that exhibit fission-fusion social dynamics – reducing direct feeding competition by breaking into smaller subgroups (Asensio et al. 2008; Smith et al. 2008; Hirsch and Gompper 2017). Among primates, van Schaik and Brockman (2005) describe a "switch-point" at which increased foraging effort (increasing daily travel to access increasingly widely-dispersed preferred resources) is no longer an energetically feasible response to declining abundance of preferred foods, and primates must engage in a more drastic response to scarcity: either diet-switching to fallback foods, area-switching to phenologically asynchronous habitat, or entering into torpor (van Schaik and Brockman 2005).

Orangutans

Biology and socioecology

Orangutans are frugivorous, arboreal great apes that live on the islands of Sumatra (*Pongo abelii* and *P. tapanuliensis*) and Borneo (*P. pygmaeus*) (Fig. 1) (Mackinnon 1974; Galdikas 1985b; Galdikas 1988; Xu and Arnason 1996; Warren et al. 2001; Nater et al. 2017). All species of orangutans have slow life histories: females first reproduce at around 15 years old, and interbirth intervals are around 7.6 years long (van Noordwijk et al. 2018). Furthermore, male orangutans exhibit extreme bimaturism wherein there are two different morphs of sexually-mature males: "flanged males" have prominent secondary sexual characteristics (cheek flanges, throat sacs, and larger body size), while "unflanged males" lack these characteristics and more closely resemble adult females in size and shape (Mackinnon 1974; Kingsley 1982; Smith and Jungers 1997).

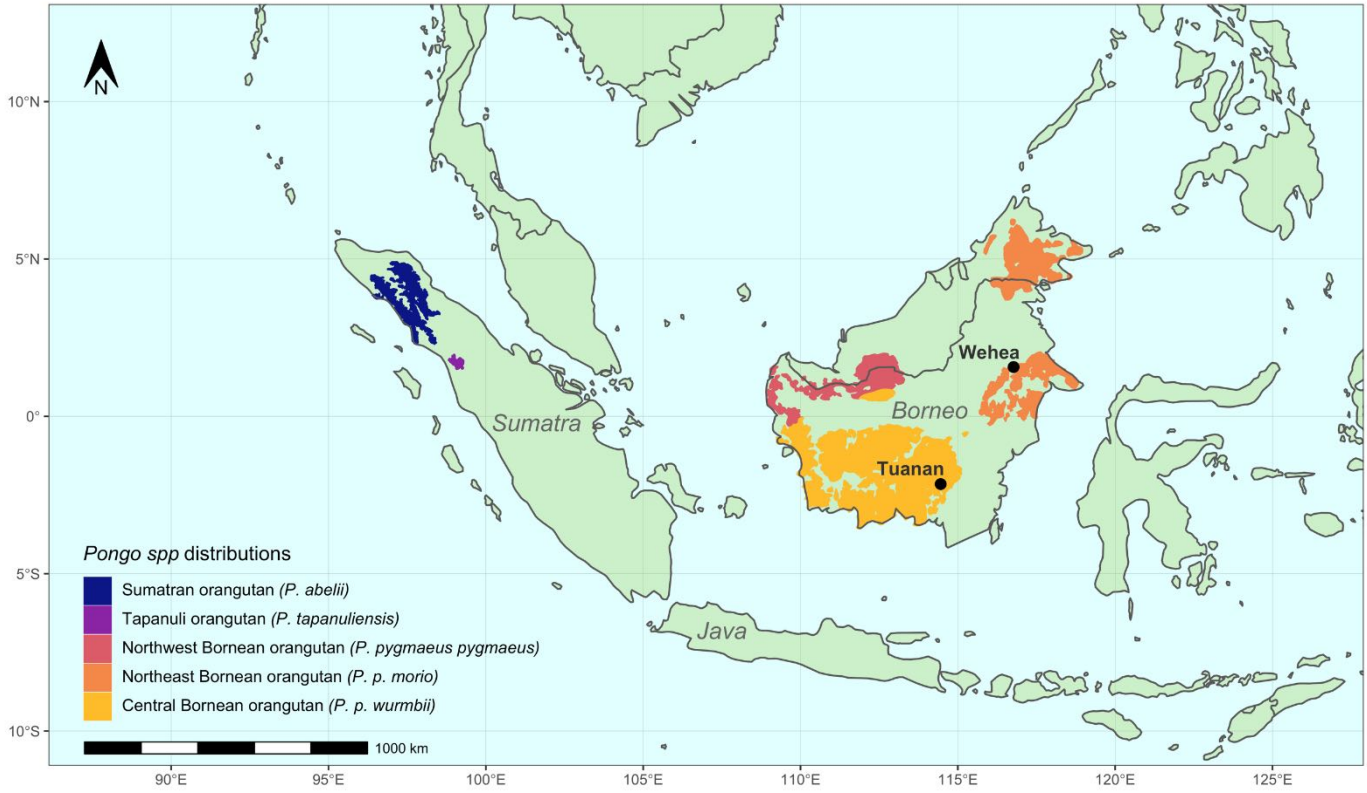

Figure 1: A map of the distribution of wild *Pongo spp* populations across Borneo and Sumatra. The two study sites included in the subsequent chapters' analyses are marked on the map (Tuanan and Wehea). *Pongo spp* distributions sources: IUCN Red List of Threatened Species (*P. abelii* – Singleton et al. 2017; *P. tapanuliensis* – Nowak et al. 2017; *P. pygmaeus* – Ancrenaz et al. 2016). Map created in R v3.5.1 (R Core Team 2018), using the rnaturalearth (South 2017), sf (Pebesma 2018), ggplot2 (Wickham 2016), and ggspatial (Dunnington 2018) packages.

Orangutans are the world's largest predominantly arboreal mammals (Thorpe and Crompton 2009). Nevertheless, orangutans in Borneo – where tigers (*Panthera tigris*) are extinct – come down to the ground occasionally to access particular resources (termites in dead logs, salt-licks), and to move (MacKinnon 1974; Galdikas 1979; Rodman 1979; Thorpe and Crompton 2009; Matsubayashi et al. 2011; Loken et al. 2013; Ancrenaz et al. 2014;

Loken et al. 2015). Ground-use occurs much more seldom in Sumatra – where tigers are sympatric over almost the entire range of orangutans (Goodrich et al. 2015; Singleton et al. 2017). Orangutans' arboreality likely contributes to their low extrinsic mortality by keeping them out of reach of most natural predators (Jones 2011; van Schaik and Isler 2012), lowering their exposure to (intestinal) parasites and other pathogens (Woodford et al. 2002), and more recently, lowering their risk of exposure to human activity (Ancrenaz et al. 2014).

Orangutans are semi-solitary and exhibit individual-based fission-fusion social organization, with the only long-term cohesive social units consisting of mothers and their dependent offspring (Galdikas 1985b; van Schaik 1999). Despite their limited gregariousness, studies have shown that female orangutans form 'clusters' – maternally-related females whose ranges overlap and who preferentially associate with each other (Singleton and van Schaik 2002; Knott et al. 2008; Singleton et al. 2009; Arora et al. 2010; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Arora et al. 2012) – while adult males roam widely in search of receptive females and areas with high fruit availability (Galdikas 1985a; Galdikas 1985c; Utami-Atmoko et al. 2009; Dunkel et al. 2013; Spillmann et al. 2017). It is not possible to delineate discrete communities among orangutans, but rather, they live in 'neighborhoods', vast social networks that function on large spatial and temporal scales, and within which individuals exhibit preferential association and avoidance patterns with their conspecifics (Kappeler and van Schaik 2004; van Schaik et al. 2009; Wich et al. 2009; van Noordwijk et al. 2012; Spillmann et al. 2017).

Within-site behavioral observations have suggested (Mackinnon 1974; Galdikas 1985; Singleton and van Schaik 2002; Knott et al. 2008), and within- and between-site genetic studies have confirmed, that orangutans exhibit female philopatry and male-biased dispersal (Mackinnon 1974; Galdikas 1985b; Singleton and van Schaik 2002; Knott et al. 2008; Arora et al. 2010; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Arora et al. 2012; Nater et al. 2013). Female orangutans live in relatively small (compared to males), generally-stable home ranges that overlap with those of other females, including their maternal kin, as well as non-kin (Knott et al. 2008; Morrogh-Bernard 2009; Singleton et al. 2009; van Noordwijk et al. 2012). Males, on the other hand, disperse from their natal areas, and then may adopt variable ranging strategies that fall anywhere along a spectrum from maintaining vast home ranges (larger than any single study area) to possibly being predominantly nomadic (Singleton and van Schaik 2001; Utami et al. 2002; Nietlisbach et al. 2012; Dunkel et al. 2013; Buckley 2014; Spillmann et al. 2017). Neither male nor female orangutans maintain exclusive territories and inter-individual space-use overlap is generally high (Singleton and van Schaik 2002; Wich et al. 2009; Spillmann et al. 2017), although female core area defense has been found in one population of wild orangutans (Knott 1998).

Because of their large body size and their preference for ripe, usually limited, fruit, orangutans accrue a high cost of association with conspecifics from direct feeding competition (van Schaik et al. 2009; Wich et al. 2009; Kanamori et al. 2016). There are also potential costs of association due to aggressive interactions with antagonistic conspecifics – aggressive fights resulting in wounds, and – on one occasion – death, have been observed between both male and female orangutans (Galdikas 1985b; Marzec et al. 2016). In general, unrelated females limit their association time together, and are more likely to have agonistic interactions (Knott et al. 2008; van Noordwijk et al. 2012; Marzec et al. 2016) compared to maternally-related females, who preferentially associate with one another, exhibit higher social tolerance, and allow their dependent offspring to engage in social play (Knott et al. 2008; Singleton et al. 2009; van Noordwijk et al. 2012). It has been shown that immature orangutans benefit greatly from the sociality of their mothers, with associations between mothers and other

conspecifics providing offspring with not only social play partners, but also social learning opportunities (van Noordwijk et al. 2012; Schuppli et al. 2016). Immatures show increased evidence of socially-mediated skill learning and, after observing known, related, conspecifics, rather than strangers, they practice the observed skills (C. Schuppli, unpublished data). Thus, despite being predominantly solitary, female orangutans' high lifetime site fidelity and clustering with maternal kin allow them and their offspring to accrue certain important social benefits.

Geographic variation

Wild orangutan populations occur on the Southeast Asian islands of Sumatra (Indonesia) and Borneo (Indonesia and Malaysia) (Fig. 1), in many different forest types (Delgado and van Schaik 1999; Wich et al. 2009). Across their geographic range, orangutan habitats differ in the amount and predictability of fruit availability, the preferred food resource of orangutans, due to several factors. Overall, fruit production is consistently higher in the west (Sumatra) than in the east (Borneo) (Marshall et al. 2009b; Wich et al. 2011), and forest type and altitude are also important factors: lower altitudes and peat swamp forests have relatively high and stable fruit production over time, whereas higher altitudes and dryland forests, such as dipterocarp forests, show relatively low and more variable fruit production (Wich et al. 2011; Wich et al. 2013). Much of the variation in forest type has to do with the degree to which different forest habitats are affected by El Niño/Southern Oscillation (ENSO) cycles: lowland dipterocarp forests – and especially those in eastern Borneo – are strongly affected by ENSO events (Curran et al. 1999; Wich and van Schaik 2000; Sakai 2002). These forests experience supra-annual masting events every 2 to 6 years, brought on by the drought, high irradiation, and lower night-time temperatures associated with El Niño events (Ashton et al. 1988; Curran et al. 1999; Wich and van Schaik 2000). During these masting events, trees of the family Dipterocarpaceae, as well as many other taxa, all flower and seed, and then later fruit, in synchrony (Wich and van Schaik 2000; Sakai 2002). Dipterocarp forest fruit productivity in between these supra-annual masting events can be exceptionally low (Sakai 2002). Thus, Bornean orangutans – especially those living in Eastern Bornean and/or in dryland dipterocarp forests – experience extremely variable fruit availability characterized by long periods of scarcity punctuated with short periods of plenty (Wich et al. 2011).

The drought caused by El Niño has another important effect on Southeast Asian forests: the drier-than-normal conditions interact with forest-degrading human activities and exacerbate fires set to clear forest land, leading to widespread wildfires (Siegert et al. 2001; Wooster et al. 2012; Meijaard 2018). Recently, the 2015/16 El Niño event was the strongest on record during the 21st century (Lim et al. 2017), and led to devastating wildfires across Southeast Asia, including Borneo, from July to November 2015 (Miettinen et al. 2017). Southeast Asia experienced high smoke exposure from July to October 2015, with the most intense haze occurring in September and October (Koplitz et al. 2016; Erb et al. 2018). Several studies have demonstrated a clear link between such wide-spread forest fires, the smoke haze that they produce, and a reduction in plants' photosynthetic capacity and thus a reduction in forest fruit productivity (Davies and Unam 1999; Calder et al. 2010; Stiegler et al. 2019). Thus, ENSO cycles affect forest fruit productivity directly – by triggering mast seed production and thus seedling establishment – and also indirectly – by drying out forests and making them more susceptible to burning, which in turn causes haze, which limits forest fruit production. In summary, there are many sources – from habitat type, to the direct and indirect effects of ENSO cycles – of spatial and temporal variation in the forest fruit production of orangutan habitats.

Orangutans exhibit morphological, physiological, and behavioral variation, much of which can be linked to this aforementioned variation in their habitats (van Schaik et al. 2009). At one end of the spectrum, Northeast Bornean orangutans (*P. pygmaeus morio*) have a highly variable amount of fruit in their diet, the smallest brains, the most robust jaw morphology, and are the least gregarious (Taylor and van Schaik 2007; Morrogh-Bernard et al. 2009; Taylor 2009; van Schaik et al. 2009). At the other end of the spectrum, Sumatran orangutans (*P. abelii*) have the least variable amount of fruit in their diet, the largest brains, and are the most gregarious (Wich et al., 2004; 2006; Taylor and van Schaik 2007; van Schaik et al. 2009). Central Bornean orangutans (*P. p. wurmbii*) appear to be intermediate on most accounts (van Schaik et al. 2009) – except for brain size which is closer to Sumatran orangutans (M. A. van Noordwijk, unpublished data; A. Nurcahyo unpublished data), and there is a lack of information available about Northwest Bornean orangutans (*P. p. pygmaeus*). In accordance with this observed phenotypic variation, Mattle-Greminger et al. (2018) found positive selection for genes linked to cardiac activity and the efficient usage of energy resources in Northeast Bornean orangutans, and genes linked to brain development and learning and memory processes in Sumatran orangutans.

An important effect of variation in forest fruit production between orangutan habitats is its influence on orangutan population densities. There is a strong positive correlation between orangutan population density and the amount and stability of a forest's fruit production: mosaic habitats and those with less extreme periods of fruit scarcity support consistently higher orangutan population densities (Marshall et al. 2009b; Husson et al. 2009). Thus, overall, we see that orangutans living in more fruit-abundant and fruit-stable habitats (at the high end of this spectrum are peat-swamp forests in Sumatra) generally have higher population densities, and are more gregarious, than orangutans living in fruit-scarce or fruit-unpredictable habitats (at the low end of this spectrum are dryland dipterocarp forests in East Borneo) (Marshall et al. 2009b; van Schaik et al. 2009; Schuppli et al. 2017). The degree of gregariousness in a population, in turn, has strong effects on orangutan culture and cognition: orangutans living in more gregarious populations have more opportunities for social learning and this correlates with larger learned skill repertoires of individuals and larger cultural repertoires of populations, including such cognitively demanding skills as tool-use for extractive foraging (van Schaik et al. 2009; Schuppli et al. 2016; Schuppli et al. 2017).

CONTENTS

The overarching aim of this dissertation is to gain a better understanding of the factors that influence and shape orangutans' movement and space-use. This dissertation deals with issues of movement and home ranges, philopatry and dispersal, and ranging responses to resource scarcity. Each chapter has a different focus, and each investigates some aspect(s) of orangutan movement and space-use on a different scale – from a micro-level investigation of ground versus canopy-use (Chapter 1), to a longitudinal perspective of female orangutan home range establishment (Chapter 2), to an inter-population comparison of female responses to fruit scarcity (Chapter 3). The influence of habitat resource availability is factored into every analysis and is an important component of each study. As such, a secondary aim of this dissertation is to investigate the influence of fruit availability on orangutans' movement and space-use, with a focus especially on adult females.

Field Sites

Data used in these chapters come from two different wild Bornean orangutan study sites in Indonesia: Tuanan in Central Kalimantan, and Wehea in East Kalimantan (Fig. 1). The Tuanan study area is composed of homogeneous, formerly selectively-logged, peat-swamp forest, which, under normal conditions, experiences within-year seasonal fluctuations in fruit availability that are relatively predictable, with only short periods of low fruit availability (see Vogel et al. 2016 for details). The Tuanan area is inhabited by a dense Central Bornean orangutan (*P. p. wurmbii*) population (van Schaik et al. 2005), who are generally well habituated to human observers. Data presented in this dissertation from Tuanan were collected primarily through direct observation focal follows between 2003 and 2017 (field project directed by Dr. Maria van Noordwijk, University of Zurich, Dr. Sri Suci Utami-Atmoko, Universitas Nasional, and Dr. Erin Vogel, Rutgers University).

In contrast, the Wehea region in which this research was conducted consists predominantly of relatively undisturbed lowland dipterocarp forest, which experiences extreme long-term fruit scarcity (S. N. Spehar and R. Delgado, unpublished data), with marked supra-annual masting events. The Wehea area is inhabited by a relatively sparse population (1.0-2.0 individuals/km^2; AMA and S. N. Spehar, unpublished data) of Northeast Bornean orangutans (*P. p. morio*) who are not habituated to human observers. Data presented in this dissertation from Wehea were collected by indirect observation using motion-triggered camera traps, between 2012 and 2017 (directed by (2012-2014) Dr. Brent Loken, Simon Fraser University, and (2014-2017) Alison Ashbury, University of Zurich, and Dr. Stephanie Spehar, University of Wisconsin-Oshkosh).

Chapter Summaries

Chapter 1

The primary aim of Chapter 1 was to better understand when and why arboreal Bornean orangutans come down to the ground. Between 2013 and 2015, several studies sought to quantify orangutan terrestriality using camera trapping: Loken et al. (2013; 2015) and Ancrenaz et al. (2014) all reported high rates of ground-use by orangutans at several study sites based on capture rates of ground-level camera traps. The common suggestion was that orangutans use the ground to cross canopy gaps, although this hypothesis is only variably supported. Despite anecdotal mentions of orangutan ground-use in broader studies of orangutan behavioral ecology (e.g. MacKinnon

1974; Galdikas 1979; Cant 1987), there was a lack of in-depth, detailed study of orangutan ground-use in any population of habituated (directly-observable) wild orangutans. In Chapter 1, therefore, I sought to identify the major causes of terrestriality among a habituated natural population of Central Bornean orangutans (*P. p. wurmbii*) inhabiting a peat-swamp forest with contiguous canopy cover. I first investigated the potential biases in ground-use in the behavioral observation data that may stem from habituation effects or observation difficulties. Next, I examined the behavioral, environmental, and spatial correlates of ground-use, with a focus on diet, development, travel speeds, and socially-motivated reasons for ground-movement. Finally, I summarized the results of ground-level camera trapping done in the Tuanan study area, thus allowing for a comparison between my study, and the aforementioned camera trapping studies which inspired it.

Orangutans at Tuanan spent, on average, a little over 2% of their time on the ground. A primary reason for ground use at Tuanan was to acquire and consume insects – all age-sex classes would descend to the ground to feed on termites from dead and rotting logs. Importantly, I found evidence of an innate aversion to terrestriality that immature orangutans had to 'unlearn' – a dependent offspring under 6 years old was more likely to cling to his/her mother when she was on the ground versus while she was in the trees, and as a dependent offspring matured and became increasingly independently mobile, he/she was less and less likely to accompany his/her mother to the ground. I did not find significant evidence that fruit scarcity leads to a higher proportion of ground-use – suggesting that orangutans at Tuanan do not use terrestriality to access fallback foods and/or to conserve energy while travelling. However, flanged males (the largest age-sex class of orangutans) spent the most time on the ground of any age-sex class, and were also the most likely to travel on the ground. Furthermore, when flanged males moved at least partly on the ground, they moved significantly faster than when they moved entirely through the trees. These two observations combined suggest that there may be some energetic benefit to ground travel. Interestingly, I observed that orangutans may use terrestrial travel – which is much less conspicuous than canopy travel – to end unwanted associations and evade conspecifics (as well as human observers). This suggests that ground-use may also have an important social function.

Chapter 2

The primary aim of Chapter 2 was to better understand *how* and *where* young female Bornean orangutans (*P. p. wurmbii*) establish their home ranges. Previous cross-sectional studies had shown that adolescent female orangutans exhibit increased sociality and temporary home range expansion prior to their first pregnancy (Galdikas 1985b; Galdikas 1995; Singleton and van Schaik 2001), and that parous adult females live in home ranges that overlap highly with their female maternal relatives – i.e. they are philopatric (Singleton and van Schaik 2002; Knott et al. 2008; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Arora et al. 2012). In this study, I therefore sought to elucidate the process of home range establishment which would tie these two previous findings – hyper-social adolescent wanderings and female philopatry – together. I used detailed longitudinal data of four young female orangutans to trace changes in their socio-spatial patterns as they matured from dependent offspring to primiparous adult females. Specifically, I investigated changes in daily travel distances, home range sizes, home range overlap with other adult females, association time with adult males and other adult females, and rate of agonistic social interactions with other adult females, as these four young females developed and matured. By combining social and spatial analyses which answer questions of how and where a

young female establishes her home range, I was able to gain a better understanding of the mechanisms of female philopatry among orangutans.

I found that a young female goes through an 'exploration phase' – characterized by longer day journey lengths and an increase in range size – which begins when she is an independent immature, and continues through her adolescence (while she is sexually active but not yet able to conceive) until she is pregnant with her first offspring. This exploration phase is facilitated by high fruit availability – in the case of one young female who became independent during a period of particularly low fruit availability, she did not show the same increase in day journey length or range size as the other young females who became independent under normal fruiting conditions. Interestingly, multiparous females did not exhibit the same increase in day journey length or range expansion leading up to pregnancy, suggesting that this 'exploration phase' is unique to pre-adolescence and adolescence, and not simply associated with the onset of a sexually active phase.

Within mother-daughter dyads, the daughter and her mother each maintained a high degree of overlap with the daughter's natal range, but they gradually shifted their ranges away from each other's and decreased their degree of range overlap as the daughter matured. By the time she was a sexually active adolescent, the daughter and her mother shared as much overlap as the daughter did with other related adult females, although she continued to associate more with her mother than with other related adult females, even after the birth of her first offspring. At this time, when the daughter was a primiparous adult female, she lived in a range that had a high degree of overlap with her original natal range and also included some new surrounding area. Her mother also maintained a high degree of overlap with the daughter's natal range, however the mother did shift, and also included some new areas into, her range. Furthermore, I found, when controlling for a daughter's phase of development and her relationship (mother, related, unrelated) to the other adult female, that a daughter's degree of range overlap with other adult females was significantly positively correlated with habitat fruit availability. This lends further evidence to the role of fruit availability in facilitating movement and shared use of space among female orangutans.

Chapter 3

The primary aim of Chapter 3 was to investigate variation in ecological strategies used to cope with resource scarcity among orangutans, and specifically to test the criteria that lead to a ranging response, rather than a dietary response, to scarcity. Studies have shown that the common response to fruit scarcity among orangutans is to 'fallback' onto non-fruit resources, including flowers, leaves, inner bark, and pith (Morrogh-Bernard et al. 2009; Vogel et al. 2009; Bastian et al. 2010; Campbell-Smith et al. 2011). However, my preliminary observations in an East Bornean mixed dipterocarp forest suggested seasonal absences of local females, and the possibility of long-distance travel in response to scarcity (Ashbury et al. 2017). I therefore compared the influence of fruit scarcity on the ranging patterns of female Bornean orangutans living under two different long-term ecological conditions: 1) relatively stable, predictable seasonal fluctuations in fruit availability with widespread high-quality fallback foods at the Tuanan site, and 2) long periods of extreme fruit scarcity with occasional supra-annual masts at the Wehea site. By comparing home range sizes and other measures of space-use among female orangutans at Tuanan and Wehea, it was possible to gain a better understanding of the conditions which lead to wider ranging – and even area-switching – in response to scarcity in preferred resources.

The results of the first comparison (Tuanan pre-scarcity versus scarcity) showed that female orangutans living in the peat-swamp forest of Tuanan significantly reduced the size of their home ranges during a period of uncharacteristically prolonged low fruit availability caused by the haze of widespread forest fires. This suggests that they were engaging in a dietary response to this scarcity episode, incorporating more ubiquitous fallback foods into their diets, and contracting their ranges accordingly. In contrast, the results of the second comparison (Tuanan versus Wehea) strongly suggests that female orangutans at Wehea – who experience long-term fruit scarcity between dipterocarp masting events – may rely on a ranging response in order to cope with fruit scarcity, travelling long distances in search of fruit and/or higher quality fallback foods. This is supported by evidence of individual female orangutans at Wehea being recorded by camera traps in locations that are significantly farther apart than locations at which individual female orangutans at Tuanan would have been recorded by comparable methods. Indeed, the evidence showed at least one adult female orangutan at locations which are, to my knowledge, farther apart than any locations ever previously reported for an individual female orangutan (over 8 km, even in the most conservative analysis scenario). I conclude that female orangutans at Wehea employ this ranging response because of the duration and severity of resource scarcity at this site, and that this response may be facilitated by the fine spatial grain of the habitat and their propensity for energetically low-cost ground travel, and further enabled by the low population density which allows for females to move unimpeded through the habitat without risk of agonistic encounters.

DISCUSSION

The results of each study are discussed at length within each chapter. However, there are some important topics which can best be understood by considering the analyses and results of all three chapters combined. Here, I discuss underlying functions, and implications, of terrestrial travel; the potential influence of population density on responses to scarcity and ranging patterns among female orangutans; some potential explanations behind the observed geographic variation in orangutan movement and ranging patterns; and the implications of my results for orangutan conservation.

Terrestrial travel

The functions of terrestriality among orangutans, including several possible functions of ground movement – more energy-efficient travel, less risk of falling, and the ability to move quickly and cryptically to evade conspecifics – are discussed in Chapter 1. The discussion of ground movement in Chapter 1 focusses on flanged males, as they are the age-sex class at Tuanan that spent the most time moving on the ground. Nevertheless, although not discussed in Chapter 2, the proportion of the day spent on the ground is included as a fixed effect in the models of young nulli/primiparous and of multiparous females' day journey lengths. Interestingly, the proportion of a day that she spends on the ground was significantly correlated with the distance that she moves that day for the young females, but not for their multiparous mothers. Although the age categories are delineated differently in Chapters 1 and 2, there is some indication in Chapter 1 that this correlation could be driven by adolescent females moving on the ground more – suggesting that ground movement is also faster and/or more efficient for not only flanged males, but also smaller bodied orangutans. Adolescent females spent more time (median = 4% of their active time) than adult females (median = 1% of active time) on the ground – possibly because adult females avoid the ground more due to the presence of their vulnerable offspring. Furthermore, adolescent females spent almost 20% of their ground time moving, while adult females spent only around 10% of their ground time moving. This may mean that adolescent females spend enough time moving on the ground that this makes a significant contribution to increasing the distance that they travel, whereas adult females spend only negligible amounts of time on the ground moving, and therefore it has no effect on their day journey lengths. Taken together, this lends more evidence to the theory that ground travel is less energetically expensive, and generally faster, than canopy travel. Which is the cause and which is the effect – i.e. do orangutans wanting to move farther come to the ground to travel, or do orangutans who choose to travel on the ground end up moving farther? – however, remains uncertain. A study investigating orangutans' cognitive mapping – for example, combining a detailed analysis of the distribution of food resources in the habitat and individual orangutans' movement choices between these resources – could begin to tease apart these two scenarios. Likewise, it would be rewarding to study differences between adolescents and adult females with infants in diet quality, as the efficiency and speed of ground travel should lead to a higher-quality diet among adolescents.

Another likely function of ground travel among orangutans is social: because orangutans are able to move quickly on the ground without disturbing vegetation and making noise, orangutans at Tuanan were able to flee unwanted associations and evade their conspecifics (and observers) by moving on the ground. This was also true at Wehea, where observers often lost unhabituated focal orangutans when they would descend suddenly to the ground and flee (AMA, personal observation). Using ground movement to flee or evade unwanted attention from conspecifics

has been observed among other arboreal primate taxa as well: among spider monkeys, males have been observed to approach females over the ground, evading their detection before attacking, and spider monkeys have also been observed to flee on the ground from agonistic encounters (Campbell et al. 2005; Valero et al. 2006). Furthermore, male spider monkeys (Aureli et al. 2006) and chimpanzees (Watts and Mitani 2001; Amsler 2009) conduct raids into the territories of neighboring groups; during these raids, males move silently along the ground in single file, rarely stopping to feed or rest, and pausing often to scan and listen. Interestingly, these other primate taxa in which ground movement has been observed when/where individuals wish to move cryptically and undetected by their conspecifics, are also taxa with fission-fusion social systems, as in orangutans. This suggests that there could be a link between fission-fusion social dynamics and cryptical travel: in taxa where an individual's knowledge of their group members' current statuses may not be up-to-date due to fissioning, cryptic travel – the ability to sneak up on one's conspecifics – may be a necessary part of an individual's behavioral repertoire.

My results strongly suggest that there is geographic variation in the frequency of ground-use, especially ground travel, between different orangutan populations. Indeed, camera trapping results from Tuanan (Chapter 1) showed a much lower rate of ground use compared to camera trapping at Wehea (reported in Loken et al. 2013; Ancrenaz et al. 2014), especially among adult females with dependent offspring. Interestingly, it may be the rate of terrestrial travel which drives this difference: in a small study of direct observation of ground use by an adult female and her adolescent son at Wehea, I showed that they did not spend significantly more time on the ground than Tuanan orangutans (Ashbury et al. 2016, Appendix 1). However, the adult female at Wehea spent significantly more of her time on the ground moving, and significantly less of her time on the ground feeding, than the adult females at Tuanan (Ashbury et al. 2016, Appendix 1). This suggests that canopy structure – which is very different between the two habitats – may play a role in encouraging ground travel: where Wehea has a lower tree density, larger and less compliant tress, and a higher canopy, it may be more challenging and energetically costly to locomote through the canopy, thus encouraging ground travel. Furthermore, at Wehea, camera traps were placed on ridgelines and logging roads (Loken et al. 2013; Loken et al. 2015). These topographical and human-made features are pathways along which animals can locomote with minimal barriers and obstructions – the presence of such features may either encourage orangutans to travel along the ground, and/or at least concentrate the areas along which orangutans do travel on the ground. At Tuanan, however, without such clear terrestrial pathways, ground travel may be less common, and also more dispersed and thus harder to capture on camera.

Predation pressure may also influence geographic differences in orangutan ground-use. The continued presence of sympatric tigers (*Panthera tigris*) in Sumatra (Wibisono and Pusparini 2010) is likely a reason why Sumatran orangutans are hardly ever observed on the ground (Rijksen 1978; C. Schuppli, personal communication). Indeed, even unhabituated Sumatran orangutans move into the highest tress and build a nest or wait (C. van Schaik, personal communication), rather than attempt to evade observers on the ground, as occurs commonly at Wehea. Within Borneo, where tigers are extinct, it could be that differences in clouded leopard (*Neofelis diardi*) densities are at least partly responsible for driving differences in ground-use rates. Indeed, this could also be a reason why flanged males use the ground more than other age-sex classes: as the largest bodied orangutans, they are the least vulnerable to predation by clouded leopards. Within contiguous forests, there is little evidence to suggest that differences in forest structure with respect to canopy gaps lead to differences in ground-use rates, though where

orangutans have reason to traverse open terrain (due to forest clearing and/or fragmentation), orangutans will use the ground in order to traverse open terrain (e.g. the case of Sumi, the adult female whose home range was burned, discussed in Chapter 1). Between population differences in the propensity for ground travel may also influence differences in the ecological strategies used to cope with habitat fruit scarcity.

Landscapes of social risk

In Chapter 3, I focussed on the effects of fruit availability on female orangutan ranging and space-use. I showed that, at Tuanan, when fruit availability is uncharacteristically low for a prolonged period, adult females reduce the size of their home ranges and likely diet-switch to ubiquitous fallback foods. I found further evidence of this link between fruit availability and home range size in Chapter 2 as well: there was a positive correlation between a young female's phase range size, as well as the dyadic overlap indices between a young female's range and other adult females' ranges, and the mean fruit availability of that phase. There are two possible pathways by which reduced fruit availability may lead to a reduction in female home range size and inter-female home range overlap: A) reduced fruit availability may increase feeding competition and therefore increase agonism between adult females, and thus adult females shrink their ranges in an effort to avoid each other, and this is facilitated by the availability of ubiquitous fallback foods to which they diet-switch; or, more directly, B) reduced fruit availability causes females to diet-switch to ubiquitous fallback foods which can be harvested over small spatial areas, thus precluding the need for large ranges, and therefore female ranges shrink. Although I cannot establish exactly which pathway is at play here, there is some evidence to suggest that the social avoidance component (included in pathway A) is non-negligible.

In Chapter 2, I found that one of the four young focal females, Mawas, did not experience the same home range expansion at the onset of independent ranging, as the other 3 young females exhibited. Indeed, the area of Mawas's home range actually decreased from dependence to independence. Importantly, Mawas transitioned from a dependent to an independent immature in February 2016, which was towards the beginning of the "scarcity" period caused by the haze of the 2015 wildfires. Thus, even when I expected to see an increase in home range size – perhaps brought on by hormonal or innate developmental factors – this expansion was suppressed in the presence of, or prevented by, low fruit availability. I suspect that the reason why Mawas did not explore and expand her home range as expected is primarily social; in theory, Mawas could diet-switch and fallback to eating the ubiquitous kamunda vines (the primary fallback food at Tuanan) anywhere – i.e. she could diet-switch but still explore. This suggests that another factor – likely social – was at play, and her range contraction may actually have been driven by attempts to avoid, or at least limit, encounters with other adult females who may be more aggressive during this time of higher feeding competition. Increased aggression during this prolonged period of fruit scarcity was documented by Meric de Bellefon et al. (in prep.), and lethal aggression between female orangutans has been documented at Tuanan (Marzec et al. 2016), which lends further evidence for the potentially important role of social avoidance to mitigate the risk of being aggressed in causing female home ranges to shrink during periods of fruit scarcity. Mawas's lack of exploration could also continue into adolescence if fruit availability were to stay low, as she may continue to be reluctant to move into areas occupied by other adult females and this may be further exacerbated by her having less access to adult males with whom to explore, as they leave this area when fruit availability is low (see Spillmann et al. 2017).

If social avoidance is indeed a major driver of the shrinking home ranges during the period of fruit scarcity at Tuanan, this has potential implications for explaining the ranging response to scarcity observed at Wehea, and the lack thereof at Tuanan. In Chapter 3, I conclude that female orangutans at Wehea employ a ranging response that resembles some degree of area-switching in response to scarcity because of 1) the duration and severity of the scarcity episodes, 2) the low costs of accessing potential phenologically asynchronous habitat (due to the topography of the area, and their propensity for ground travel), and 3) the very sparse population which limits inter-individual competition costs and lessens the risks of agonistic associations with other females in the new area. Given the potential role that social avoidance plays at Tuanan, I speculate that the third criterion for area-switching at Wehea – low populations density and therefore low risk of encountering aggression from other females – is of particular importance, not only in *enabling* long-distance ranging at Wehea, but also in *preventing* a ranging expansion at Tuanan. This highlights the important role that population density plays in influencing spatial behavior among orangutans: in a dense population, it is advantageous to stay put and diet-switch to whatever is available, whereas in a sparse population, it is advantageous to go and search for better alternative food sources. Of course, the presence of decent quality and ubiquitous fallback foods at Tuanan (kamunda vines, as opposed to just inner bark and leafy vegetation) is intricately linked with this site's high population density as it likely increases the carrying capacity of the habitat even during seasonal scarcity. Thus, I speculate that the presence of decent quality and ubiquitous fallback foods in a habitat not only *enables* diet-switching among orangutans, but it actually *inhibits* area-switching by supporting a high population density, and thus increased risk of social aggression. Figure 2 demonstrates these two different (not mutually exclusive) pathways through which ubiquitous and decent quality fallback foods may lead to diet-switching.

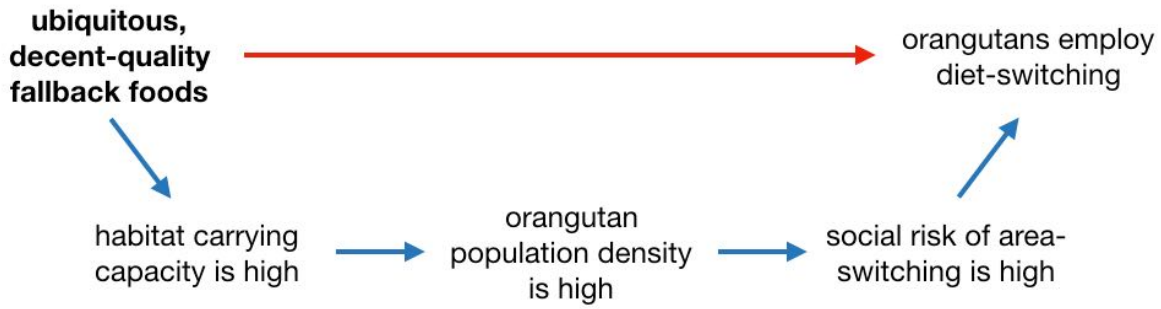

Figure 2: The pathways through which ubiquitous, decent-quality fallback foods may lead to diet-switching among orangutans. The red arrow represents the direct pathway, while the blue arrows represent the pathway which accounts for the social risk of an alternative strategy (area-switching) in a densely populated habitat.

To tease apart which of these two pathways is the largest driver of diet-switching among female orangutans, further study is needed. If indeed high population density has a significant inhibitory effect on area-switching, we could expect to see this effect in other contexts as well. For example, it is possible that the exceptionally high inter-generational site-fidelity among females at Tuanan (Chapter 2) is – to some extent – maintained by the high population density. Given the opportunity, young females may explore farther and potentially establish their home ranges in areas which are new to them, and not overlapping (or overlapping less) with their mothers'. However, because of the high density of females in the Tuanan area, and the social risks of ranging among non-relatives,

young females remain strictly philopatric and establish ranges that overlap substantially with their mothers and maternal relatives. Released rehabilitant orangutans may provide some clues as to the ranging behavior of females in 'empty' habitats: at the Batikap release site in Central Kalimantan – a habitat which is mostly devoid of wild orangutans – of approximately 64 independent/adult females who were released at this site between 2012 and 2014, only 23 females could be monitored for 12 months post-release (Lokuciejewski 2019). Of these 23 monitored females, only 14 established home ranges near the release site, while the others were classified as "commuters" (occasionally observed in the study area) and "wanderers" (dispersed from the study area) (Lokuciejewski 2019). Although it can be problematic to draw conclusions about wild orangutan ranging behavior based on the ranging patterns of rehabilitant orangutans – which can be heavily biased by the locations of provisioning, human activity, and individual orangutans' past experiences with humans (A. Marzec, personal communication) – these observations at Batikap suggest that females may not have a strong innate predisposition to 'staying put', but rather – where the social landscape, i.e. population density allows – be inclined to disperse and move across long distances. Further study, such as a detailed investigation of the degree of mother-adult daughter home range overlap across sites, with a large enough sample size to control for differences in diet quality, could help to elucidate whether or not population density has a strong effect on the degree of transgenerational site-fidelity among maternally-related female orangutans.

Geographic variation

The variation observed between orangutans at Tuanan and at Wehea may not be entirely caused by Bornean orangutans' phenotypic plasticity and thus their proximate responses to ecological differences between the two habitats, but rather they could also be related to genotypic variation. An innate, subspecies difference between the orangutans at Tuanan (*P. p. wurmbii*) and Wehea (*P. p. morio*) which drives their differing rates of ground-use and responses to scarcity cannot be ruled out. The different lineages of Bornean orangutans (*P. pygmaeus*) may have diverged as recently as 176 ka (Arora et al. 2010; but see Warren et al. 2001), but there are significant morphological differences between the *P. p. wurmbii* and *P. p. morio* subspecies (Taylor and van Schaik 2007; van Schaik et al. 2009; Taylor 2009), suggesting significant variation between these two subspecies. Thus, differences observed between these two subspecies at Wehea and Tuanan could be, at least in part, attributable to innate, evolved, genetic differences. Interestingly, however, *P. p. morio* (such as at Wehea) have more robust jaw morphology and smaller brains, suggesting that they are better adapted to diet-switch to fallback foods (Taylor 2006; Taylor and van Schaik 2007). In other words, if these differing responses to scarcity were driven entirely by genetic differences, we would expect to observe *P. p. morio* at Wehea diet-switching to low quality, difficult to process foods, for which they have specific morphological adaptations. I therefore suggest that differences in responses to scarcity between these two sites are driven by Bornean orangutans' behavioral plasticity and proximate responses to differences in local ecologies.

I further suggest that there may be a strong cultural component to differences in ranging behaviors among these two populations. It is well established that different orangutan populations have different behavioral repertoires (van Schaik et al. 2003), and that learned skills are shared and passed on between individuals through social learning (Jaeggi et al. 2010; Schuppli et al. 2016). Indeed, even accounting for differences in genetics and ecology, behavioral variation between populations of orangutans cannot be fully explained, thus suggesting that culture plays a strong role in shaping their behavior and local adaptations (Krützen et al. 2011). It is quite possible

that differences in movement and ranging patterns between Wehea and Tuanan orangutans – e.g. frequency of ground travel, ranging response to scarcity – are cultural behaviors, maintained through social learning. With respect to ground-use and terrestrial travel, at Tuanan, there is evidence of an innate weariness of the ground, and a reluctance of young dependent offspring to accompany their mothers when they move down to the ground. At Wehea, on the other hand, camera trap photos of adult females almost always include dependent offspring – either clinging or following along behind – many of whom are big (old) enough to be independently mobile and therefore not accompany their mothers to the ground if they didn't want to (as observed at Tuanan, Chapter 1). This suggests that young orangutans at Wehea may unlearn their innate weariness of the ground very early in life, as their mothers continue to travel on the ground despite the presence of their small clinging offspring. In this way, ground-use, and in particular ground travel may be a cultural adaptation at Wehea, shaped by the local ecology.

Implications for conservation

The three orangutan species are all listed as critically endangered by the IUCN Red List of Threatened Species (IUCN 2019). These studies have important implications for orangutan conservation, especially with respect to landscape planning and orangutan translocation efforts. Landscape planning should seek to avoid isolating forest fragments between unpassable habitats, especially in regions with highly variable fruit production (such as East Borneo) where I have shown that individuals employ area-switching and need far larger areas in order to sustain themselves. Forest corridors – or at least land-use types that allow for orangutan movement (e.g. plantations, as opposed to urban areas or open mines) – should be maintained, or – where necessary – cultivated, in order to ensure that both male and female (in the case of wide-ranging populations such as Wehea) can move across the landscape. This is important in order to maintain not only gene flow, but also to enable individuals to achieve their dietary requirements where/when resources may be scarce. Furthermore, where forest fragments are surrounded by plantations, education and training for plantation workers is important in order to minimize orangutan killings. Proper monitoring of orangutans found in plantations would allow for the determination of which individuals are just passing through these areas (and should be left alone) and which are sustaining themselves on plantation resources only and thus having a negative economic impact, requiring further intervention (such as translocation) by trained professionals.

Translocation efforts – moving wild orangutans from high-risk areas to better protected habitats – especially of female orangutans, should be undertaken only with extreme caution and consideration. Translocating a female orangutan from one population into another may put her at risk of extreme aggression from local resident females, especially where a population already has a high density. Furthermore, repeated translocations into the same habitat may lead to local over-crowding, thus increasing the social risk of wide-ranging movement and inhibiting females' ability to search for fallback resources if fruit is scarce or insufficient. Because it is also possible that scarcity-coping strategies, such as diet-switching, area-switching, and even ground travel (to conserve energy and/or facilitate area-switching) are culturally transmitted behaviors – which vary from one population to another – translocated orangutans would not necessarily have the correct learned skill repertoires to be able to cope with fluctuations in fruit availability in their new habitats. At the very least, translocation should only ever take place into sparse populations, and where possible, individuals should be monitored post-release in order to ascertain their success in adapting to their new location.

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Chapter 1: Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan

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ABSTRACT

Orangutans (genus *Pongo*) are the largest arboreal mammals, but Bornean orangutans (*P. pygmaeus spp.*) also spend time on the ground. Here, we investigate ground use among orangutans using 32,000 hours of direct focal animal observations from a well-habituated wild population of Bornean orangutans (*P. p. wurmbii*) living in a closed-canopy swamp forest at Tuanan, Central Kalimantan, Indonesia. Ground use did not change with increasing observation time of well-habituated individuals, suggesting it was not an artifact of observer presence. Flanged males spent the most time on the ground (ca. 5 % of active time), weaned immatures the least (around 1%). Females and immatures descended mainly to feed, especially on termites, whereas flanged males traveled more while on the ground. Flanged males may travel more inconspicuously, and perhaps also faster, when moving on the ground. In addition, orangutans engaged in ground-specific behavior, including drinking from and bathing in swamp pools. Supplementary records from 20 ground-level camera traps, totaling 3986 trap days, confirmed the observed age-sex biases in ground use at Tuanan. We conclude that ground use is a natural part of the Bornean orangutan behavioral repertoire, whereas it remains unclear to what extent food scarcity and canopy structure explain population differences in ground use.

KEYWORDS**:** Borneo, orangutan terrestriality, *Pongo pygmaeus wurmbii*, ground travel, direct observation, camera trapping

INTRODUCTION

Orangutans (genus *Pongo*) are the only great apes found outside of Africa and are the largest habitually arboreal mammals. There are two recognized species of orangutans, *P. abelii* in Sumatra and *P. pygmaeus* in Borneo (Brandon-Jones 2004; Nater et al. 2011). Both orangutan species have very slow life histories, with late ages at first reproduction and extremely long interbirth intervals (Galdikas and Wood 1990; Wich et al. 2004; Knott et al. 2009). Their arboreality contributes to their low extrinsic mortality by keeping them out of reach of most natural predators (Jones 2011; van Schaik and Isler 2012). Indeed, orangutans in Borneo – where tigers (*Panthera tigris*) have been extinct for millennia – are known to occasionally come down to the ground in natural forests (Wallace 1869). In contrast, terrestrial behavior among Sumatran orangutans – where the range of extant tigers overlaps almost the entire range of orangutans (Chundawat et al. 2011; Singleton et al. 2008) – has hardly ever been observed (Thorpe and Crompton 2009). Other possible selective pressures to maintain an arboreal lifestyle include a relatively lower exposure to (intestinal) parasites and other pathogens by being away from the ground, and more recently, a lower risk of exposure to human activity (Woodford et al. 2002; Ancrenaz et al. 2014).

Many behavioral studies have noted terrestrial activity by orangutans (e.g. MacKinnon 1974). In the Bornean studies, the large-bodied flanged males are reported to travel more frequently on the ground than females or smaller unflanged males (Galdikas 1979; Rodman 1979; Thorpe and Crompton 2009), whereas Sumatran flanged males do not use the ground (Thorpe and Crompton 2006), except in emergencies, such as when fleeing from an opponent (Cant 1987; van Schaik 2004). Travelling terrestrially may be beneficial for several reasons, including a reduced risk of falling if a supporting tree or branch breaks (Kehoe and Chan 1986; Kraft et al. 2014). Terrestrial travel is also thought to be less energetically expensive than arboreal travel, even for an ape anatomically adapted to arboreal travel (Cant 1987; Begun and Kivell 2011; Loken et al. 2013), and because the cost of climbing is directly proportional to body size (Thorpe et al. 2007), this would explain the observed ground-use bias towards the large flanged males. This economical travel option may allow flanged males to offset certain costs associated with their secondary sexual characteristics (for instance, their inability to keep up with fleeing females), and thus diminish the advantages of the unflanged stage (van Schaik et al. 2009; Dunkel et al. 2013). Therefore, the Borneo - Sumatra contrast in predation pressure and degree of terrestriality may have affected inter-island differences in social organization and patterns of male developmental arrest.

This argument assumes that the animals' behavior is not influenced by the presence of human observers. Thus, an observed orangutan may use the ground less in the presence of an observer because the observer is perceived as a threat (Loken et al. 2013), or alternatively over time may come to use the ground more in the presence of an observer because their presence is perceived as an indication that the ground is safe (Grundmann 2006; Russon et al. 2009).

Three recent studies have sought to investigate and quantify orangutan terrestrial behavior using indirect observation through ground-level camera traps. Loken et al. (2013), Ancrenaz et al. (2014), and Loken et al. (2015) reported frequent detection by camera traps of Bornean orangutans on the ground at several sites, including varying types of forest subjected to varying degrees of human disturbance. These camera-trap studies have convincingly shown that in the absence of human observers, (flanged) males use the ground rather frequently.

However, the other age-sex classes were also recorded to be on the ground, albeit less frequently in most (Ancrenaz et al. 2014; Loken et al. 2015), but not all sites (Loken et al. 2013).

The frequency of ground use found in these camera-trap studies has led to much speculation about the proximate reasons why wild orangutans descend to the ground. If the forest structure allows, orangutans are capable of crossing considerable gaps in the canopy by tree swaying, which is often energetically less costly than descending to the ground and climbing up again (Thorpe et al. 2007; Manduell et al. 2011). Thus, terrestriality for the sole purpose of crossing canopy gaps should rarely be efficient. Nevertheless, some recent studies have emphasized terrestriality especially to cross gaps in the forest (Rijksen and Meijaard 1999; Ancrenaz et al. 2014) and have even suggested that once individuals are used to using the ground to cross canopy gaps, this would enable them to disperse across open terrain in fragmented habitat (Ancrenaz et al. 2014). Alternatively, orangutans' ground use is not forced by canopy gaps, but used to travel over longer distances in continuous forest (Galdikas 1979; Rodman 1979) or to acquire terrestrial (fallback) food, water, or minerals (MacKinnon 1974; Cant 1987; Matsubayashi et al. 2011).

To identify the major causes of terrestriality, we present direct observational and camera-trap data of ground use (defined as any time during which an orangutan is in contact with the ground) among Bornean orangutans (*Pongo pygmaeus wurmbii*) of a mostly habituated natural population, inhabiting a peat-swamp forest without major canopy gaps. We first investigated whether the behavioral data show a strong bias due to habituation or observation difficulties. Then we examined the behavioral, environmental and spatial correlates of ground use. Finally, we summarize the evidence of orangutan ground use from camera traps in our study area.

METHODS

Study Site

Behavioral data were collected from July 2003 to July 2010 on the natural population of Bornean orangutans in the Tuanan Orangutan Research Area, Mawas Reserve, Kalimantan Tengah, Indonesia (2° 09' S; 114° 26' E). The entire study area (approx. 7.5 km^2) is homogenous peat swamp forest, which has previously been subjected to selective logging, but had had (as of 2003) at least 5 years to recover (van Schaik et al. 2005). There is an approximately 200 x 200 meter grid of narrow research trails over the entire study area. A few main trails have narrow raised wooden boardwalks for part or all of their length in order to facilitate travel efficiency. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates and adhered to the legal requirements of Indonesia.

Data Collection

Individual focal data were collected from 2003 to 2010 in accordance with standardized field methods (http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html), including activities and heights recorded at 2-minute intervals (see also van Noordwijk et al. 2012; Dunkel et al. 2013). Orangutans observed to use the boardwalks were not scored as being on the ground. Location points were taken every half hour on a hand-drawn map that was later digitized (early years), or with a handheld Garmin GPSMAP 78 series GPS unit (later years). Both methods involve a certain amount of error (approximately +/- 10 meters), however because of the

large spatial scale in which orangutans move, as well as the nature of our questions, it is unlikely that this error measure has influenced our analysis.

Focal individuals could not always easily be followed without disturbing them once they were travelling on the ground through dense vegetation. Therefore, we included all focal activity data as long as the individual was followed for at least 3 hours, to reduce the bias in the data due to the focal being 'lost' on the ground. However, we used all data covering at least a half hour to calculate the speed of travel bout movement and to assess space-use.

In total, the dataset covers over 32,300 hours of focal observation on all age-sex classes of orangutans (plus an additional 5585 hours on pre-weaned offspring sampled together with their mothers) by an experienced team. In the current analyses, we distinguish between 'immatures' – all weaned immatures, whether ranging in association with their mother or independently; 'adolescent females' – ranging independently, sometimes sexually active, but nulliparous; 'adult females' – all parous females (almost all accompanied by offspring); 'unflanged males' – sexually mature males without cheek pads; 'flanged males' – sexually mature males with fully developed secondary sexual features. In addition, some analyses were done on the dependent, pre-weaned offspring (infants) with known ages.

The monthly fruit abundance index was measured as the percentage of trees (in a phenology plot of over 1500 trees) bearing fruit (cf. Marshall et al. 2009). Rainfall was measured daily at camp and minimum and maximum temperatures were measured daily at a fixed location in the forest, 50 meters from the forest edge.

Twenty camera traps (Bushnell TrophyCam, 8MP model) were installed throughout the study area, with at least 700 m between each one. The traps were active for a total of 3986 camera-trap days, between February 2010 and February 2012. The camera traps were programmed to take two photos, 10 seconds apart, whenever movement was detected. One 'camera-trap record' refers to a set of two photos, and no camera-trap records of orangutans occurred at the same station on the same day, thus all records were considered independent. Fifteen of these cameras (3174 camera-trap days) were installed facing research trails at a height of 60-80 cm off the ground. The five additional cameras were located facing the raised boardwalks (812 camera trap days). All orangutan records (N=31) were extracted and the age-sex classes of the orangutans in the photos were determined.

To control for possible observer effects, we analyzed changes in individuals' time spent on the ground over the 7-year period, as the orangutans were presumably becoming increasingly habituated to observer presence. In order to control for observation biases due to losing focal orangutans prior to the end of a full-day follow, we totaled and compared the number of times that focal individuals were followed to their night nests, lost prior to building a night nest, and lost when they were moving on the ground prior to building a night nest.

Spatial data analysis

Exact locations were known for every instantaneous data point falling on the hour and the half hour, as well as morning, day, and night nests. Approximate locations were calculated for every activity data point (2-minute interval), by equally distributing the distance between the nearest preceding and subsequent location points.

In order to investigate general ground-use spatial patterns, a grid cell analysis was first performed: all location points were overlaid onto a grid of cells measuring 200 x 200 m. Thus, the total time spent in each area (grid cell) could be compared with the time spent on the ground in each area. Second, all location points were overlaid with a map of the trail system and any points within 5 meters of a trail were categorized as "on trail" (the 5-meter buffer zone was included in order to accommodate mapping and GPS error). This allowed for a comparison of orangutans' ground use on versus off trails.

Average travel speed was calculated for all follows lasting at least 3 hours by dividing the follow path length (measured between all subsequent half-hour points) by the duration of the follow. The overall travel speed during follows that did not include any movement on the ground were then compared to the overall travel speeds of follows which did include at least some movement on the ground. A second more detailed analysis of distance travelled during specific bouts of movement included data from any follow lasting at least 30 minutes, using the 2-minute location points approximated between half-hour location points. A 'travel bout' was defined as a 30-minute period in which the individual's activity was recorded as 'Move' (locomotion in some way or other) during at least 10 (out of a maximum of 15) behavioral data points. Travel bouts began at the time and location of the first point where the point sample activity was 'Move' and ended 30 minutes later, regardless of the temporal distribution of the 10+ 'move points' during that time. If an orangutan continued to travel, and had at least 10 move points in the next 30-minutes, this was classified as a second travel bout. The distance traveled during these bouts was measured as the total distance travelled, from 2-min point to 2-min point, from the beginning to the end of the 30-minutes. Travel bouts were then classified as having occurred entirely through the trees or as having included at least some ground travel, and the travel bout distances for the two groups were compared.

Statistical analyses

All data were analyzed using chi-squared tests, Pearson's correlations, Kruskal-Wallis tests, and Wilcoxon signed-rank tests. For the Kruskal-Wallis and the time budget (activity and food items) Wilcoxon signed-rank tests, all data for each individual throughout the entire study period were summed, and individuals' scores were grouped by age-sex classes. For the kiss squeak analysis, as well as the average travel speed and the travel bout distance Wilcoxon signed-rank tests, each individual's mean scores were used, grouped by age-sex class where applicable (using median scores did not affect any of the conclusions). Thus, in order to avoid pseudo-replication in the data due to repeated sampling of the same individuals, each individual is represented by one data point in the analyses comparing time budgets, kiss squeak frequencies, travel distances, and speeds. Where simple statistical tests were not applicable, we have presented our results using descriptive statistics or as anecdotes. Camera-trap data are all described quantitatively, as were data investigating whether or not individuals' ground-use frequencies changed significantly over time as they became increasingly habituated to human observer presence.

RESULTS

Potential biases and habituation effects

Long-term data consistently suggest that even habituated orangutans seem wary to descend to the ground when observers are present, and emit 'kiss squeaks' – apparently toward observers – more frequently when they are close to or on their way to the ground than when they are higher up in the canopy. In order to analyze kiss squeak frequency without habituation level as a confounding factor, we used only data collected from 2006 to 2010, i.e. after 2-3 years of habituation, on the 7 most frequently encountered and thus most habituated females. For each follow series lasting 5 to 10 days, the proportion of 2-minute intervals when the focal was on or at <5 m from the ground and emitted a kiss squeak and the proportion of 2-minute intervals when the focal was >5 m off the ground and emitted a kiss squeak was calculated. Even though observers always attempted to remain at a respectful distance, these females kiss squeaked significantly more often when they were <5 m above the ground than when they were >5 m above the ground (Wilcoxon signed-ranks test: $Z=28$, $P<0.05$, $N=14$, $r=-0.54$).

We also looked for bias in the observational data due to terrestrial behavior. Focal individuals were 'lost' before they made a night nest in 17% of all 3215 follows. This was most often because the focal individuals were on the ground and could not be followed through thick vegetation where visibility wass low but following too closely would disturb them and human locomotion is necessarily slow (N=331 times, or 60% of the lost cases). However, flanged males were much more frequently lost overall, and they were also twice as often lost while on the ground than females, immatures or unflanged males ($X^2=272.81$, df=4, $P<0.001$; see Fig. 1.1).

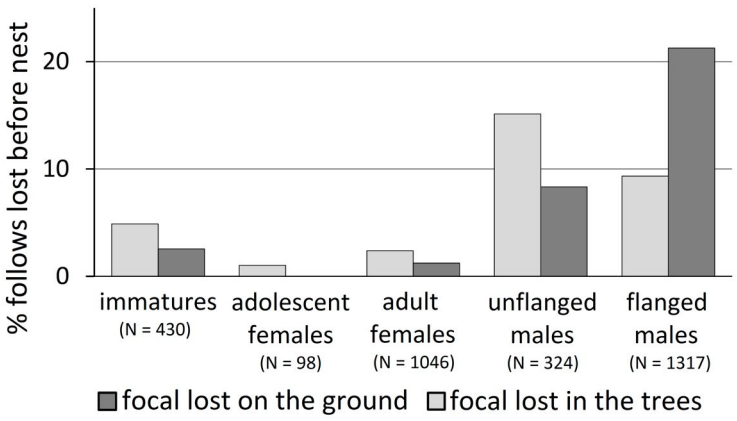

Figure 1.1: The percentage of follows in which the focal individual was lost in the trees (light grey) and lost on the ground (dark grey) before making a night nest. The total number of focal follows started (either from morning nest or found during the day) is indicated per age-sex class.

To examine whether focal orangutans gradually change their patterns of terrestriality in the presence of observers (i.e. long-term habituation effect), we compared the yearly proportion of ground use after 2-3 years of habituation, for 4 adult females for whom we had at least 200 hours of focal data per year during multiple years. Figure 1.2 shows that there was no consistent pattern in time spent on the ground as these individuals became increasingly familiar with human observer presence over the years. Thus, the observations of the well-habituated individuals provided relatively unbiased estimates of their natural ground use. However, we did not include data collected on unhabituated individuals, trying to flee or hide from observers or giving distress vocalizations for extended periods.

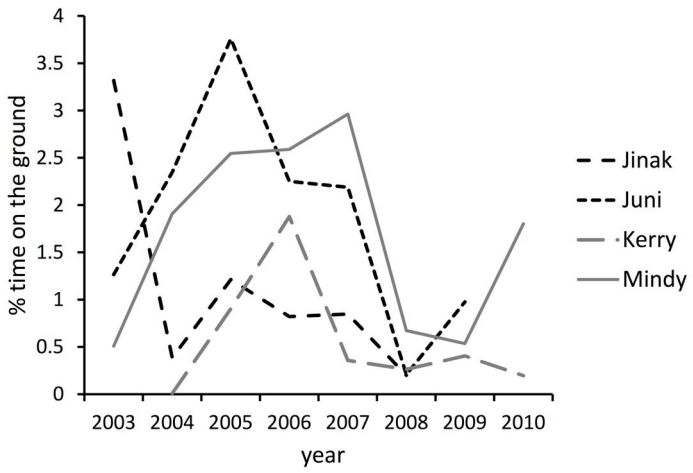

Figure 1.2: The percentage of time spent on the ground by habituated females for whom >200 hr of focal data was available for at least 4 different years (all individuals, as well as the combined Pearson correlations are not significant, P>0.10).

Frequency and behavioral correlates of ground use

Tuanan orangutans spent, on average, 2.29% of the total focal observation time on the ground. When including only those individuals for whom there were over 200 hours of data (total: N=25; immatures: N=2; adolescent females: N=2; adult females: N=8; unflanged males: N=6; flanged males: N=7), there was a significant difference between age-sex classes in the proportion of time spent on the ground (Kruskall-Wallis test: $H(4)=11.85$, $P<0.05$) and post-hoc tests reveal that the only significant differenc was between adult females and flanged males: flanged males spent significantly more time on the ground than did adult females (Fig. 1.3). Note, that other pairings' differences were likely not significant primarily because of the small number of included individuals in the immature (N=2) and adolescent female (N=2) age-sex classes.

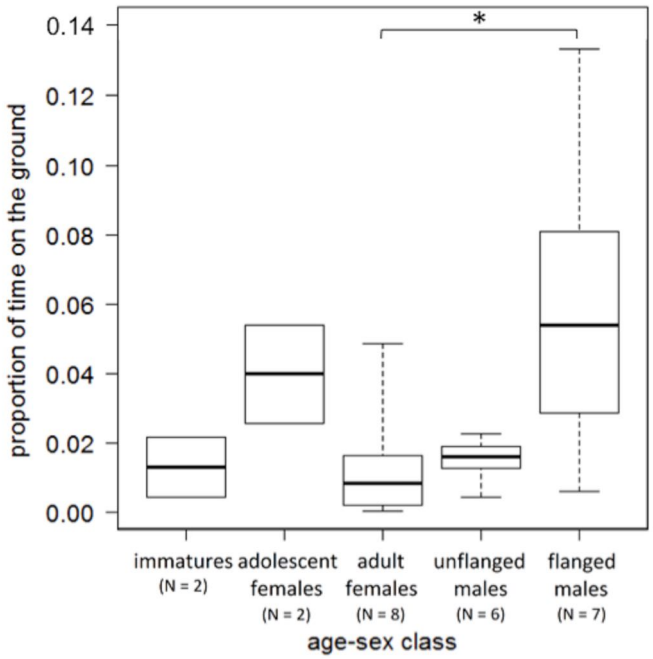

Figure 1.3: The proportion of time during which individual habituated focal individuals were on the ground, by age-sex class. Center lines represent medians, and whiskers extend to the maximum and minimum values of the data (*P<0.05).

When the study started in 2003, an adult female (Sumi) with a young offspring was found in the logged and burned area adjacent to the study forest. Since there were only a few (mostly dead) trees still standing in her presumed original home range, this female mostly foraged and moved on or close to the ground in the dense and low recovering vegetation (this also made it difficult to follow her without being too close, so the sample is likely an underestimate of her actual time on or close to the ground). Over the next three years, this female moved completely into the forested study area, where she spent only ca 1 % of her time (close to the average for mothers with dependent offspring) on the ground *vs.* >12 % of her time on average during her first full year of being studied. Thus, whereas circumstnaces forced her to use the ground often in the early years of this study, she became more arboreal and avoided being on the ground again when she had the opportunity.

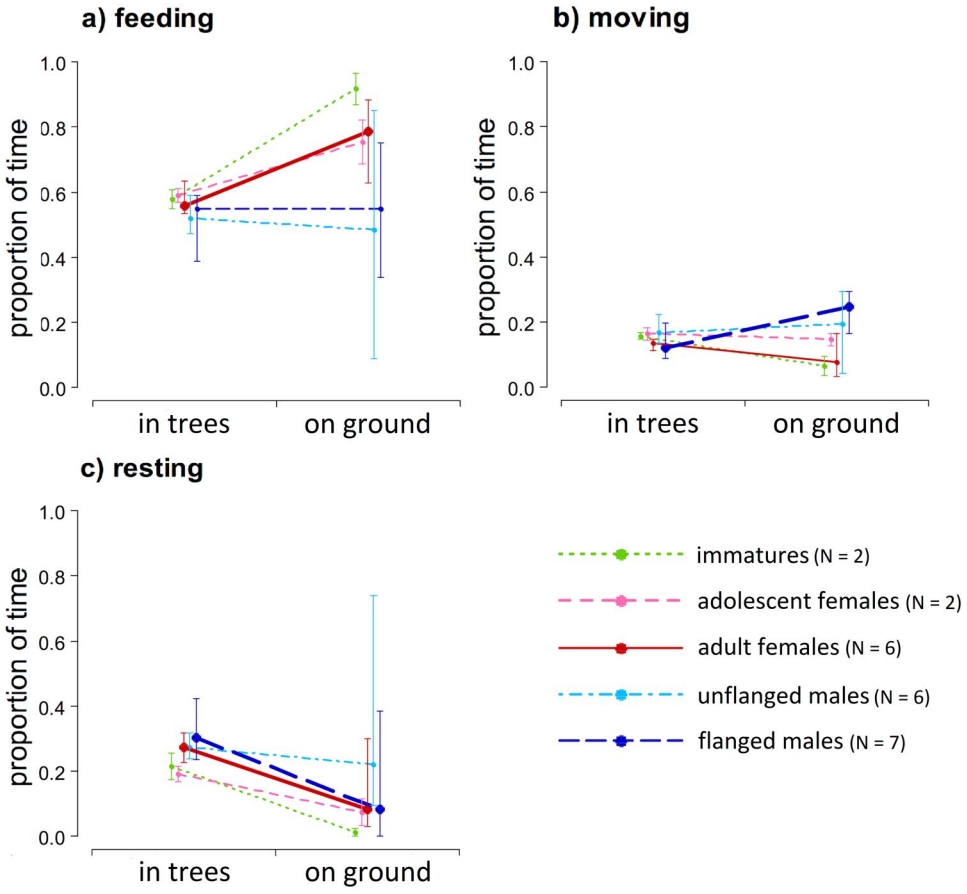

Figure 1.4: The difference in proportion of time that focal individuals spent feeding (a), moving (b), and resting (c) while in the trees versus on the ground, by age-sex class. Proportion of time spent engaging in each activity is the proportion of the total time spent on that substrate (ground or trees). Thicker lines denote significant differences ($P<0.05$).

We also compared activity budgets and diet composition on the ground versus in the trees. This analysis only included individuals for whom we had at least 200 hours of data and who were observed to spend at least one hour on the ground (immatures: N=2; adolescent females: N=2; adult females: N=6; unflanged males: N=6; flanged males: N=7). A comparison of focal individuals' activity budgets when on the ground versus in the trees (Fig. 1.4) showed that adolescent and adult females, as well as immatures, spent a greater proportion of time feeding and a smaller proportion of time resting when on the ground. Indeed, this difference was significant for adult females

(Wilcoxon signed-ranks test: (feeding) Z=21, P<0.05, N=12, r=-0.62; (resting) Z=21, P<0.05, N=12, r=-0.62). Flanged males spent a greater proportion of time moving when on the ground (Wilcoxon signed-ranks test: Z=28, P<0.05, N=14, r=-0.65), and reduced their proportion of time spent resting when on the ground (Wilcoxon signed-ranks test: Z=2, P<0.05, N=14, r=-0.53). Unflanged males had the same activity profile in the trees and on the ground.

The diet composition of all age-sex classes while on the ground differed from that while in the canopy: all orangutans spent much more time feeding on insects, mostly termites, which are found in decaying wood (Fig. 1.5). This difference was significant for flanged and unflanged males (Wilcoxon signed rank tests: (flanged males) Z=28, P<0.05, N=14, r=-0.65; (unflanged males) Z=21, P <0.05, N=12, r=-0.62). In addition, all orangutans more often drank water while on the ground, even though water was sometimes also obtained from treeholes. Wilcoxon signed rank tests showed that this difference was significant for adult females (Z=21, P<0.05, N=12, r=-0.62), flanged males (Z=27, P<0.05, N=14, r=-0.58), and unflanged males (Z=21, P<0.05, N=12, r=-0.62). With the exception of immatures, individuals also tended to spend more time feeding on vegetative plant parts (mostly mature leaves and stems for *Ficus spp.*, pith of *Pandanus spp.* and *Zingiberacea*) while on the ground, although this contrast was not significant for any age-sex class.

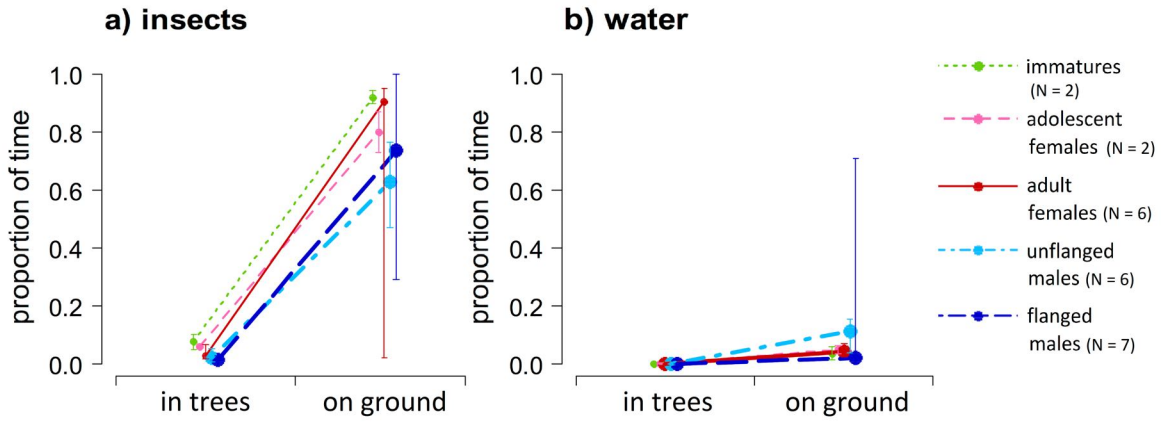

Figure 1.5: The difference in proportion of time that focal individuals spent feeding on insects (a), and water (b), while in the trees versus on the ground, by age-sex class. Proportion of time spent feeding on each item is the proportion of the total time spent feeding while on that substrate (ground or trees). Thicker lines denote significant differences (P<0.05).

It is important to note that most food items can either be also found in – or at least easily carried up into – the trees, and therefore do not actually require orangutans to stay on the ground during or after collection. Indeed, all food items except for termites, soil, and water, were more often consumed while in the trees than while on the ground, when considering absolute, rather than proportional, amount of time spent feeding on the items. Indeed, termites – which were the overall most-consumed food item while on the ground – were consumed more often in the trees than on the ground by all adult females, all unflanged males, one flanged male, all adolescent females, and all immatures. Water was more often drank while in the trees than while on the ground by 2 adult females, 2

flanged males, 1 unflanged male, and 2 immatures. Of those indivudals observed to consume soil (N=11), 2 (both adult females) consumed it in the trees, rather than on the ground.

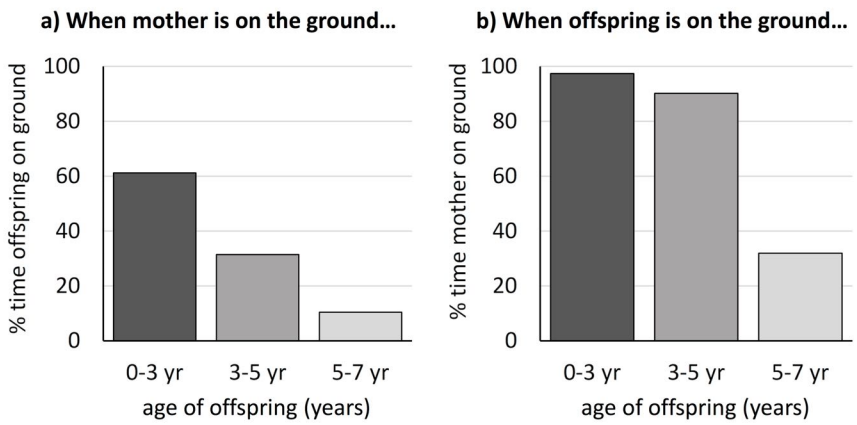

Figure 1.6: The percentage of time that a dependent offspring was on the ground while his/her mother was on the ground (a), and the percentage of time that a mother was on the ground when her dependent offspring was on the ground (b), by offspring age class.

Mothers may be more likely than other adult age-sex classes to carry termite-infested logs up into the trees. Such 'termite-logs' are often shared - that is, mothers tolerate and actively enable co-feeding by their offspring. Independently mobile offspring seemed reluctant to spend time on the ground and tended to stay behind in the trees, or climbed back up faster, when their mothers were on the ground. Figure 1.6 shows the proportion of time that a dependent offspring was on the ground when his/her mother was on the ground, and the proportion of time that a mother was on the ground when her dependent offspring was on the ground, broken down by age of the offspring. As offspring matured, they were increasingly likely to follow less closely and stay up in the trees when their mothers descended to the ground, and offspring were hardly ever on the ground without their mothers until they were at least 5 years old. In addition, even though it seems much easier for a small infant to move around on the ground than in the trees, dependent immatures up to the age of 4-5 years were consistently more likely to be clinging to their mothers while on the ground than while in the trees during maternal moving, feeding and resting (Fig. 1.7).

In contrast, some social conditions seem to encourage leaving the trees. Orangutans fleeing from conspecifics, either in response to an agonistic encounter or as a form of preventive distancing, sometimes choose to descend to the ground and then quickly move away: in 44% (28 out of 62) of observed events of fleeing, the fleeing individual did so on the ground (Fig. 1.8). After an individual fled from a conspecific on the ground, the association (proximity within 50 m) ended in 96% of the 28 cases, compared to only 68% of the 34 events when an individual fled through the trees (X^2=6.71 Yates corr, df=1, P<0.01). Furthermore, during her first years in the study area, the above-mentioned female, Sumi, disappeared over the ground whenever she encountered another orangutan, especially one of the resident females.

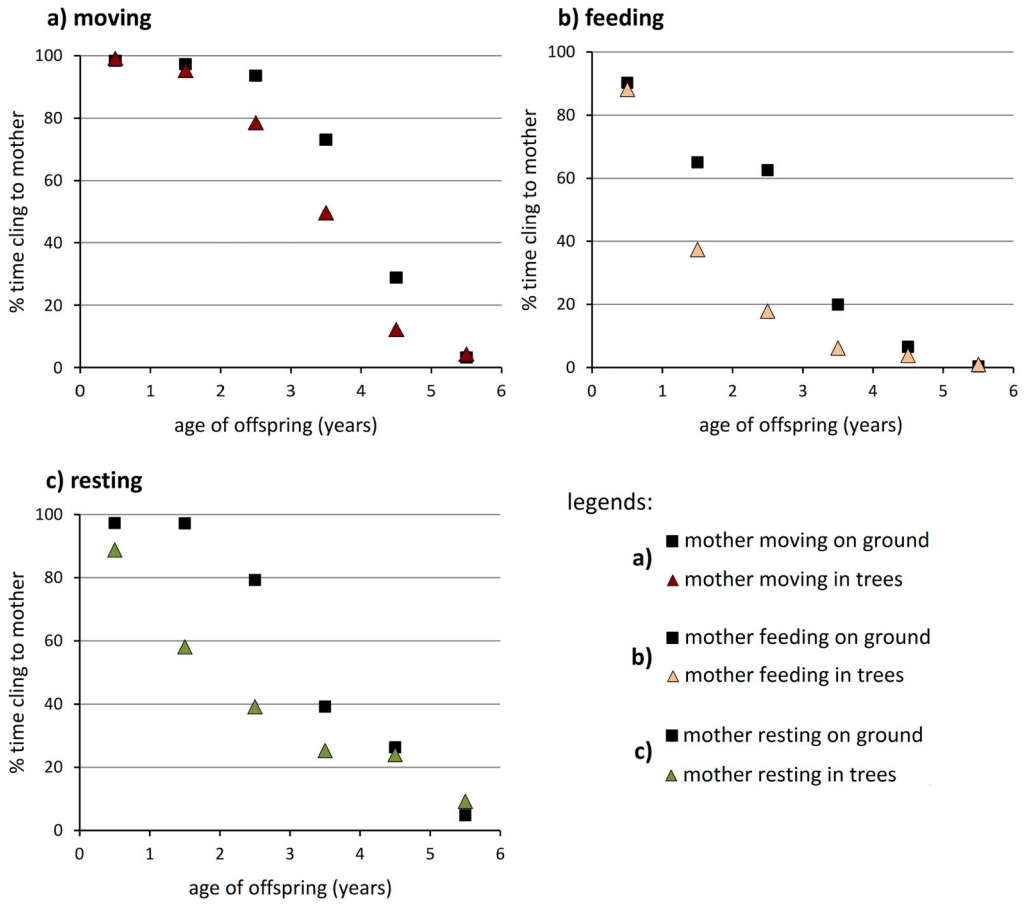

Figure 1.7: A comparison of the percentage of time that a dependent offspring was clinging to his/her mother during moving (a), feeding (b), and eating (c), while his/her mother was on the ground versus while she was in the trees, by offspring age.

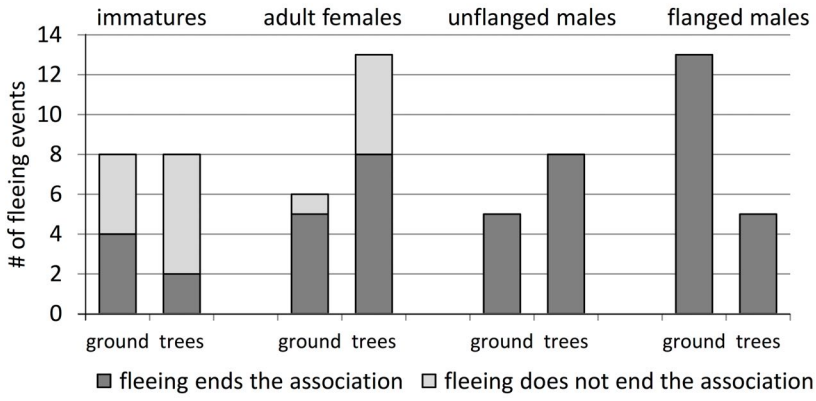

Figure 1.8: The number of observed fleeing events (from conspecifics) through the trees and on the ground, comparing cases that did not result in the termination of the association (distance between conspecifics remained within 50 m) (light grey) and those that did end the association (dark grey).

Environmental correlates of ground use

Monthly rainfall in the Tuanan swamp forest is highly variable within and between years (van Noordwijk et al. 2013). On average, the least rain falls in August and September (<100 mm/month) and the most rain falls in December to April (>300 mm/month). However, there was no relationship between the amount of rain in the

previous 60 days or 30 days (intended as a proxy measure for standing water) with the proportion of time individuals spent on the ground per focal follow (N=3428 days, N=3456 days respectively).

Average monthly maximum temperature in the forest (28.8 °C) varied little (range of monthly average: 28.1 °C in January to 29.5 °C in September). Focal individuals were occasionally seen standing or sitting in standing water on the ground, splashing themselves or even rubbing themselves with wet leaves. In total, 14 different individuals representing all age-sex classes were observed to do this at least once. Even though these individuals seemed to cool off this way, the maximum temperature (measured at a fixed location) was barely higher on days with this 'bathing' behavior than on days without it (average during focal follows with 'bathing' T_{max} 29.10 ± SD 1.64 °C, N=32 *vs.* average during focal follows without 'bathing' T_{max} 28.72 ± SD 1.58 °C, N=3706) and well within the measuring error of our thermometers. Thus, although many different Tuanan orangutans seemed to use standing water for apparent comfort behavior, the frequency of this was very low (at least in the presence of observers) and not clearly related to weather conditions.

During periods of food scarcity, orangutans may be expected to increase their time spent on the ground, either in order to collect fallback foods or to save energy by travelling longer distances over the ground. However, there was no consistent effect of fruit availability on the proportion of time that individuals spent on the ground, using the averages per age-sex class (based on at least 50 hours) per month. Adolescent females (the age-sex class with the smallest sample) were the only age-sex class to show a significant correlation. However, it was in a direction opposite to the expected one: as fruit availability increased, the time they spent on the ground also increased (Pearson's r=0.695, N=12-month samples of ≥ 50 hr, P<0.05). Most age-sex classes with larger samples (including immatures, unflanged and flanged males) showed the expected negative trends, as did lumping all class samples together, but all of these thrends were non-significant, (Pearson's r= -0.080, N=198-month samples, P>0.10).

Spatial distribution of ground use, and speed of ground travel

Orangutans spent time on the ground in all parts of the study area, and overall, did not favour ground use in particular areas. There was a postive correlation between the total number of location recordings and the number of on-the-ground location recordings in each grid cell of the study area (Pearson's r=0.69, N=282, P<0.001). There were two noticeable outliers – grid cells in which orangutans spent more time than expected on the ground. In these cells (which are adjacent), orangutans spent a relatively high proportion of time feeding on termites (66.2%, 84.5%). This suggests that the spatial distribution of termites has a large influence on the spatial distribution of orangutan ground use.

Overall, orangutans were within 5 meters of a research trail in 8.4% of all on-the-ground observations, and in 9.0% of all above-ground observations. Flanged males were occasionally observed to move on the ground along trails; however, there were no significant differences between ground use on and off trails for flanged males or any other age-sex class, except for independent immatures, who were significantly less likely than expected to be on a trail when on the ground (X^2=4.79, df=1, P<0.05).

Among flanged males, the overall speed of travel during follows of at least 3 hours which did not include any ground travel was significantly lower than for those which did include at least some ground travel (Wilcoxon signed-rank test: Z=10, P<0.005, N=32, r=-0.57). Furthermore, among flanged males, the distance travelled during 30-minute travel bouts was significantly farther during bouts that did include some ground travel than bouts which took place entirely through the trees (Wilcoxon signed-rank test: Z=21, P<0.05, N=12, r=-0.62) (Fig. 1.9). It is important to note, however, that even the distances travelled by flanged males during 30-minute travel bouts that took place entirely on the ground (no travel through the trees at all) (N=3, range=97-498 meters) did not exclusively exceed the maximum distance travelled by a flanged male during a 30-minute move bout taking place entirely through the trees (428 meters). No other significant relationships between speed or distance travelled and movement on the ground were found for any age-sex class, over entire follows or during specific travel bouts.

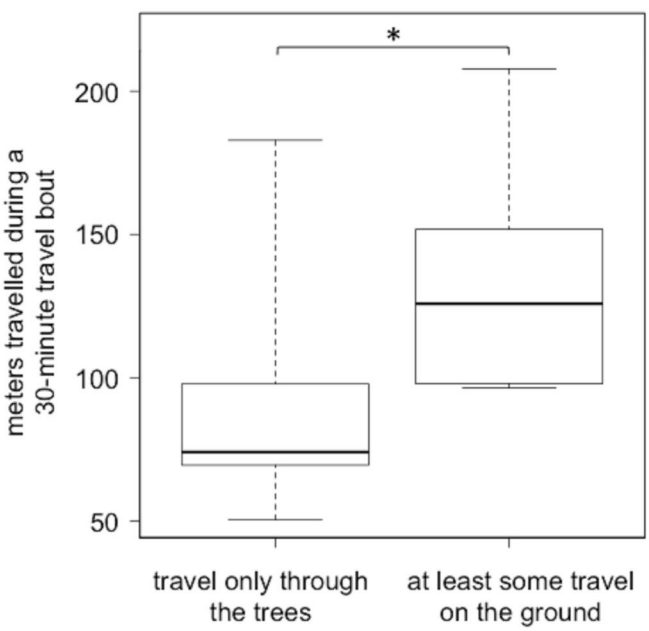

Figure 1.9: The difference in distances travelled during 30-minute travel bouts which occurred entirely through the trees versus those which included some ground use, for flanged males only (N=6). Center lines represent medians and whiskers extend to the maximum and minimum values of the data (*P<0.05).

Evidence of orangutan ground use from camera traps in Tuanan

Within the study area, orangutans were photographed by ground-level camera traps 19 times (on average 0.006 times per trap day). Over half (53%) of the Tuanan camera-trap records were of flanged males, while the age-sex classes of 8 orangutans in the remaining records (47%) could not be reliably determined, although all were at least adolescent size and 4 were definitely not flanged males. This means that flanged males were recorded in a minimum of 53% and maximum of 77% of camera-trap records. The additional 5 camera traps directed at raised boardwalks recorded females with offspring at least 3 times and flanged males 7 times, out of a total of 12 records – for 0.015 records per trap day. Orangutans were significantly more likely to be recorded by camera traps facing the boardwalks than by those facing the trails (X^2=5.39, df=1, P<0.05).

DISCUSSION

Reasons for ground use in Tuanan

Although, until now, behavioral studies of wild Bornean orangutans have only reported terrestriality anecdotally, it is clear that ground use is within their natural behavioral repertoire. Consistent with early reports from other studies (e.g. MacKinnon 1974; Galdikas 1979), flanged male orangutans at Tuanan spent more time on the ground than any other age-sex class. Indeed, we found that flanged males were the age-sex class most often lost by observers, often because they would descend to the ground. Therefore, our estimate of ground-use rate for flanged males is likely biased towards an underestimation. Furthermore, while flanged males often traveled along the ground, adult females primarily came to the ground to feed on certain resources, such as termites. We found no evidence of a strong spatial bias to orangutan ground use, except that orangutans forced to live in more open areas spent more time on the ground. Instead, orangutans did spend more time than expected on the ground where they could most often engage in termite feeding. Thus, ground use is not simply a response to canopy gaps or unsuitable habitat (cf. Ancrenaz et al. 2014), but occurs to satisfy specific needs.

Orangutans at Tuanan were observed to descend to the ground to collect, and sometimes consume, food items, including termites, water, and peat-soil/turf. In the homogenous peat-swamp forest at Tuanan, standing water is available and consumed throughout the study area, and there was no indication that it satisfies any nutritional/mineral needs aside from thirst (in contrast to drinking from salt lick pools as described for some other sites e.g. Matsubayashi et al. 2011).

There is nonetheless strong evidence for an innate wariness of the ground. First, resting on the ground was extremely uncommon for orangutans other than flanged males. Second, even the most habituated adult female orangutans were more likely to kiss squeak when they are on their way to, or already on, the ground. Kiss squeaks are interpreted as both alarm and mobbing calls (Hardus et al. 2009) and alert others (mostly offspring) to watch out, but also to warn potential predators (including human observers) that they have been noticed and will be chased if they come too close (Tuanan, unpublished observations on humans and a dog). Lastly, small (unweaned) immature orangutans hardly ever descended to the ground alone, and even only rarely accompanied their mothers down to the ground, unless they could cling to her body. This apparent reluctance of small immatures to spend time on the ground, even when their mothers did, may explain why adult females did not spend significantly more time feeding on termites on the ground than up in the trees, while adult males, both flanged and unflanged, did. Thus, mothers may spend less time on the ground than would be efficient for themselves, to accommodate the needs of their young offspring. Indeed, adult females with dependent offspring are often observed to descend to the ground alone, and then carry a termite-infested log back up into the trees. These termites are then consumed in the canopy, where the offspring is allowed to co-feed.

The camera-trap data confirmed these observational findings. Immatures avoided coming to the ground on trails, supporting the notion that they only leave the trees when the attraction, i.e. feeding opportunity, is strong enough and not to travel or cross canopy gaps. Adult females with dependent offspring were recorded relatively more frequently on raised boardwalks than on trails, suggesting mothers with offspring avoided travelling on the ground when possible.

This pattern suggests that there may be a learned loss of fear over the course of an individual's life: as a young orangutan increasingly often accompanies its mother to the ground, grows in body size, and becomes more familiar with ground-based resources such as termites, terrestriality becomes a more regular component of its behavioral repertoire and its natural aversion to ground use is lessened. This indicates that regular ground use among Bornean orangutans may be a relatively recent addition to their behavioral repertoire, perhaps only since the extinction of tigers on the island (which may have occurred as recently as the early Holocene (Kitchener and Dugmore 2000; Piper et al. 2007; Louys 2014)). These learned behaviors serve to increase the feeding niche of all orangutans, as well as the mobility of male orangutans.

This interpretation is bolstered by the fact that Bornean orangutans do not show obvious anatomical differences compared to their Sumatran counterparts, and thus lack any clear adaptation for terrestrial locomotion, such as the knuckle-walking capabilities of chimpanzees and gorillas. Indeed, since splitting from the common hominid ancestor, it is likely that orangutans' adaptations to arboreality have been further refined (Thorpe and Crompton 2006).

Sumatran orangutans still share their range with tigers, and indeed rarely descend to the ground, except in social emergencies or to collect food and quickly carry it up into the trees (Rijksen 1978; van Schaik 2004; in the swamp forest of Suaq Balimbing habituated females spent <0.05 % on the ground and even flanged males were <0.25 % terrestrial: C. Schuppli, personal communication). However, for both species, other predators such as clouded leopards, snakes, and wild pigs, are a potential threat especially to the smaller-bodied individuals, explaining their wariness to be on the ground (see Kanamori et al. (2012) for an example of a predation event on a juvenile orangutan). This wariness was less obvious among the large-bodied, and thus less vulnerable, flanged males, who even occasionally spent nights on the ground in Tuanan. Indeed, ground nesting by flanged males at Tuanan was observed 3 times during the study period (N=442 follows to nest), but has been observed more frequently since (in the period of 2010 to 2012: 10 out of 197 follows to nest), with one male accounting for 9 of those nights. Individuals of other age-sex classes were never observed to nest on the ground, with the exception of the adult female whose home range was burned – she was observed to spend at least 4 nights on the ground when she was still ranging in her original home range after it had been cleared (i.e. before she began to push her range into the adjacent forested area). Thus, the only individuals who ever nested (apparently) voluntarily on the ground were large-bodied flanged males.

Over the course of several hours, or even full days, flanged males travelled faster when a proportion of their movement occured on the ground. This was not seen for other age-sex classes, which may be because their terrestrial movement was often done in the context of searching for food and may therefore have been much less unidirectional than that of larger males who were using the ground more for travel without inspecting foraging options. Because location points were only recorded every half-hour, the sinuosity of individuals moving around and searching for food on the ground was not measured. Interestingly, only 4 % of adult females' 30-minute travel bouts included any ground-travel (as compared to 22 % for flanged males), showing that when adult females are engaging in relatively consistent movement (rather than that which is heavily interspersed with feeding, for example), they rarely included any ground travel.

Our analysis of distances traveled during 30-minute travel bouts shows that flanged male orangutans are able to move quickly both on and off the ground but that there is an association between including at least some terrestrial locomotion and higher speeds. However, because flanged males travelling only through the trees were often able to reach travel speeds as fast or nearly as fast as those incorporating some ground-use, it is likely that factors other than simply the potential speed of travel have a large influence over whether or not an individual moves on the ground or in the canopy.

Although Bornean orangutans do not show specific morphological adaptations for terrestrial locomotion, there was evidence that they are able to move relatively inconspicuously – even when moving quickly – along the ground. First of all, the relatively high rate at which focal individuals were lost by observers when on the ground, compared to when in the trees, demonstrates that it is much harder for humans to follow an orangutan who is moving along the ground than one who is moving through the trees. At Tuanan, orangutans on the ground hardly disturb or rustle the thick undergrowth when moving, the way that they disturb the trees when moving through the canopy. Thus, even a small distance of 5-10 meters between the focal orangutan and its observers was often enough for observers to lose sight of the orangutan entirely. Flanged males were lost on the ground more often than other age-sex classes, and thus observational data for the proportion of time spent on the ground by flanged males was likely an underestimation.

Secondly, there was evidence that losing contact with an orangutan who was moving on the ground may not be only a human problem: orangutans fleeing from conspecifics on the ground were more likely to end the association than those fleeing through the trees. Thus, at least at Tuanan – where the forest is mostly made up of small, pliable trees – fleeing over the ground may be a more effective strategy to end unwanted associations with conspecifics than fleeing through the trees, which involves noisy and conspicuous movements such as tree swaying. This all indicates that in some closed canopy forests, orangutans' travel along the ground can be less conspicuous than travel through the trees, and social factors may greatly influence whether or not an orangutan chooses to travel on the ground. In Borneo, where competition between orangutan males can frequently turn violent (Dunkel et al. 2013), it is not surprising that males often seem to attempt to move around undetected by conspecifics.

Another common hypothesis to explain ground travel over longer distances by orangutans is based on the assumption that travel on the ground is more energy-efficient than through the trees, which may require frequent directional diversions in all three dimensions (Cant 1987). This would especially be true where canopy structure and connectivity are poor. Saving energy by moving along the ground could be especially beneficial for the large-bodied flanged males, and thus explain why they are the most likely age-sex class to move on the ground and why this ground-movement is associated with higher speeds and travel over longer distances. It has been suggested that microclimate might be an additional advantage of ground travel, e.g. Takemoto (2004) found that chimpanzees spent more time on the ground during the dry season and speculated that this helps them to stay cool and thus reduces their metabolic costs associated with thermoregulation. Measurements at Tuanan (Hermann 2010) have shown that maximum temperature tends to be higher at the mid-canopy level (5 or 10m) than closer to the ground. It could therefore be speculated that, at least in the case of long-distance ground travel by the larger-bodied males, ground use increases when canopy temperature increases. However, the general patterns of ground use among Tuanan orangutans did not show a meaningful relationship with daily maximum temperature (measured at

approximately 1.3 m off the ground). Furthermore, standing swamp water was also often used for bathing. Despite this behavior seeming to cool the orangutans off, it did not specifically occur on especially hot days. Thus, it is still unclear to what extent ground travel (and use in general) aids orangutans in reducing thermoregulatory costs.

One other potential explanation for ground travel, especially for these large-bodied males, is that it may reduce their risk of falling. Orangutans at Tuanan are occasionally observed to fall – either all the way from the canopy to the ground, or within the canopy from higher up to lower down – when supports break under their weight. Evidence of long bone fractures consistent with falls out of the forest canopy has been found among great apes, including orangutans (Kehoe and Chan 1986; Kraft et al. 2014). This risk of injury from falling may be especially high for the heaviest orangutans, the flanged males, and thus may contribute to their more frequent ground travel.

Comparison with other sites

Our camera-trap data show that the frequency of orangutan terrestriality at Tuanan falls within the range of ground-use frequencies reported from other sites in Borneo (Ancrenaz et al. 2014). Of all the camera-trap study sites, Tuanan is perhaps most comparable with the Sabangau study site, in terms of forest type (peat swamp forest) and current and past management classification ("old and slightly logged forest"), as per Ancrenaz et al. (2014). Orangutan density at Tuanan is approximately 3 times higher than at Sabangau, and the total camera-trap rate of capture at Tuanan is 3 times higher than at Sabangau. This suggests that orangutans in these two similar forests may be spending comparable amounts of time on the ground.

Interestingly, the rate of camera-trap captures of orangutans on the ground from the dryland, formerly selectively logged area in Wehea Forest (Loken et al. 2013, breakdown of counts reported in Ancrenaz et al. 2014) was almost twice that of Tuanan, despite an orangutan population that is 4 times less dense. This suggests that the orangutans (*P. p. morio*) living in Wehea Forest spend far more time on the ground than the orangutans (*P. p. wurmbii*) of Tuanan. Furthermore, the camera-trap study of Loken et al. (2015) demonstrated the propensity for ground use among various age-sex classes of orangutans, including adult females with and without dependent offspring. Indeed, in all 3 forest types, adult females accounted for 41% of camera-trap records, while flanged males accounted for 23-36% of records (Loken et al. 2015). This suggests that in the areas studied by Loken et al. (2013; 2015), ground use by age-sex class may be different than among the Tuanan orangutans. Unfortunately, it is not yet possible to determine the relative contribution of structural factors (forest type, canopy structure, etc.), population/sub-species differences, or other factors, to this substantial observed difference. We suspect that food availability and distribution does play a role at this between-population scale.

In conclusion, we have shown that terrestriality is a normal component of the Bornean orangutan behavioral repertoire. In Bornean forests, even those with a relatively closed canopy, orangutans occasionally descend to the ground in response to unwanted associations, to retrieve attractive food sources (some of which, e.g. termite logs, may be carried up into the trees), and – especially in the case of flanged males – to travel. However, like Sumatran orangutans, Bornean orangutans do appear to have an innate fear of the ground. Unlike Sumatrans, though, they gradually overcome this fear during ontogeny, although females never do so completely. The proportion of time spent on the ground differs between individuals and between populations, but for now the role of food scarcity, canopy structure, or other factors remains unclear.

The tendency of Bornean orangutans to come to the ground may better equip them to deal with forest degradation. In this respect the Bornean orangutan may have more behavioral flexibility as to habitat use than Sumatran orangutans. This difference may enable Bornean orangutans to better cope in disturbed, fragmented, and human-dominated landscapes.

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Chapter 2: Home range establishment and the mechanisms of philopatry among female Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan

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ABSTRACT

Female orangutans exhibit natal philopatry, living in stable home ranges that overlap with those of their maternal relatives. Using data collected from 2003 to 2017 at Tuanan in Central Kalimantan, Indonesia, we used a longitudinal approach to better understand the mechanisms of female philopatry and the factors that influence the home range establishment process of young female orangutans (*Pongo pygmaeus wurmbii*). Data on movement and sociality were collected during nest-to-nest focal follows of individual orangutans; 4 young nulli/primiparous females, their 3 multiparous mothers, and 7 other unrelated adult females living in the same area. Our results show that a young female goes through an 'exploration phase,' beginning when she is an independent immature and lasting through her adolescence, characterized by an increase in home range size and distance travelled each day. This exploration is facilitated by high resource availability and association with adult males. A young female maintains a high degree of overlap with her natal range, but gradually decreases the degree of overlap with her mother's concurrent range. By the time she is a sexually active adolescent, a young female and her mother share as much overlap as a young female does with other related adult females, although she continues to associate more with her mother than with them, even after the birth of her first offspring. Our findings indicate that the high habitat productivity and high orangutan population density of Tuanan lead to a high degree of life-time site-fidelity and overlap among maternal kin.

KEYWORDS: Bornean orangutan, female philopatry, day journey length, home range, range overlap

INTRODUCTION

Natal dispersal patterns are a fundamental aspect of many animal mating systems; in dispersing, an animal is able to avoid inbreeding, and limit resource and intrasexual mate competition with kin (Greenwood 1980; Johnson and Gaines 1990). However, the costs of dispersal can be high: moving to unfamiliar areas has been shown to reduce feeding efficiency, increase susceptibility to predators, and limit opportunities for cooperation between kin (Bonte et al. 2011). Most mammals have evolved sex-biased dispersal: usually, males disperse before or upon reaching sexual maturity, while females remain philopatric, staying in or near their natal areas (Greenwood 1980). Philopatric animals avoid the costs of dispersal and accrue the social and ecological benefits of staying in a familiar area and group, with known kin, after independence and sexual maturity have been reached.

Among solitary animals, philopatry is defined spatially, as an individual remaining in or near its natal area rather than in its natal group (Waser and Jones 1983). Sex-biased natal philopatry among predominantly solitary mammals has been described across a wide range of taxa, including dusky-footed woodrats (*Neotoma fuscipes*; McEachern et al. 2007; Innes et al. 2012), raccoons (*Procom lotor*; Ratnayeke et al. 2002), red-necked wallabies (*Macropus rufogriseus*; Johnson 1986), otters (*Lutra lutra;* Quaglietta et al. 2013), black bears (*Ursus americans*; Rogers 1987b; Moyer et al. 2006; Costello et al. 2008; Costello 2010), brown bears (*Ursus arctos*; Støen et al. 2005), and tigers (*Panthera tigris*; Smith 1993; Gour et al. 2013). Even among predominantly solitary animals, philopatry can have social benefits. For example, Coquerel's dwarf lemurs (*Mirza coquereli*; Kappeler et al. 2002) and grey mouse lemurs (*Microcebus murinus*; Lutermann et al. 2006) both exhibit evidence of female philopatry, with female relatives clustering together spatially. Lutermann et al. (2006) suggest that, despite grey mouse lemurs' predominantly solitary nature, females may accrue certain social benefits from this philopatry as well, namely access to shared sleeping sites – important resources for predator avoidance and thermoregulation.

Many studies have investigated the processes and mechanisms of natal dispersal (ex. Johnson and Gaines 1990; Isbell and van Vuren 1996), but fewer studies have sought to understand the opposite process; that of home range establishment, and the mechanisms of natal philopatry, in solitary species. Waser and Jones (1983) suggest three mechanisms through which philopatric parents can remain solitary despite having philopatric offspring: parents can either share, split, or leave their range. Sharing one's range requires temporal, rather than spatial, avoidance between parents and offspring, and can occur only in non-territorial species. Splitting occurs when a parent bequeaths a part of its home range to its offspring, who then maintains access to this area to the exclusion of the parent (both or either may incorporate new, adjacent area into their home range). Leaving occurs when a parent bequeaths its entire home range to its offspring, and disperses to an adjacent or more distant area.

The three mechanisms described by Waser and Jones (1983) are not mutually exclusive within species or even individuals. Indeed, among black bears (*Ursus americanus*), Rogers (1987) found evidence of splitting and then leaving by mother bears: female yearlings established small home ranges within their mother's ranges that she avoided. As daughters matured, they expanded their ranges into full territories and mothers shifted their own territories away from their daughters (Rogers 1987a). Similar patterns were observed in a population of Bengal tigers (*Panthera tigris*), where daughters usually established ranges adjacent to their mothers, and in some cases, mothers even shifted their own territories to accommodate their maturing daughters' (Smith 1993). Unfortunately, little is known about the mechanisms of philopatry among other species.

Orangutans (*Pongo spp.*) are non-territorial, semi-solitary, great apes (Mackinnon 1974; Galdikas 1985). They exhibit individual-based fission-fusion social organization, with the only long-term cohesive social units consisting of mothers and their dependent offspring (van Schaik 1999). Within-site behavioral observations have suggested, and within- and between-site genetic studies have more recently confirmed, that orangutans exhibit female philopatry and male-biased dispersal (Mackinnon 1974; Galdikas 1985; Singleton and van Schaik 2002; Knott et al. 2008; Arora et al. 2010; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Arora et al. 2012; Nater et al. 2013). Female orangutans live in small (relative to males), generally-stable home ranges that overlap with those of their maternal kin, as well as with those of non-kin (Knott et al. 2008; Morrogh-Bernard 2009; Singleton et al. 2009; van Noordwijk et al. 2012).

Although female orangutans are not territorial, they probably defend core areas in one population (Knott et al. 2008). In general, unrelated females limit their association time together, and are more likely to have agonistic interactions (Knott et al. 2008; van Noordwijk et al. 2012; Marzec et al. 2016). Females preferentially associate with their maternal kin, exhibiting higher social tolerance, and allowing their offspring to engage in social play (Knott et al. 2008; Singleton et al. 2009; van Noordwijk et al. 2012). Thus, despite being predominantly solitary, female orangutans' high lifetime site fidelity and clustering with maternal kin allow them to accrue certain important social benefits associated with philopatry.

Orangutans have exceptionally slow life histories; female age at first reproduction is around 15 years, and they have the longest interbirth interval of any mammal (7.5 years) (van Noordwijk et al. 2018). A young orangutan usually remains in close association with its mother for a few years after the mother's next offspring is born (van Noordwijk et al. 2009). This slow development makes it possible to study in detail the step-by-step socio-spatial dynamics of the process of home range establishment among female orangutans, provided sufficient longitudinal data are collected. Thus, we can ask very specific questions about *how* and *where* a young female establishes her home range.

With respect to *how* a young female establishes her range, previous studies have shown that nulliparous female orangutans experience a prolonged phase of adolescent sterility prior to their first pregnancy, during which time they exhibit an increased degree of sociality and evidence of temporary home range expansion (Galdikas 1995; Singleton and van Schaik 2001). For female chimpanzees, who are usually not philopatric, Deschner and Boesch (2007) proposed the 'social passport hypothesis' to explain shorter postpartum amenorrhea and an increased number of cycles to conception among younger – and therefore usually lower ranking, less established, and/or recently immigrated – females: more swellings until conception increases the duration of young females' attractiveness to males. This extended attractivity ensures the presence and support of males, thus lessening the aggression that young females receive from older, more established females (Deschner and Boesch 2007; Kahlenberg et al. 2008), and could explain why nulliparous females who emigrate have significantly older ages at first reproduction than those who do not (Walker et al. 2018). It could be that the extended phase of adolescent sterility among female orangutans serves a similar function: attracting males and thus limiting the intolerance that these young females receive from adult females while exploring and establishing their own adult home ranges.

With respect to *where* a young female establishes her range, we can extrapolate from cross-sectional studies that suggest or demonstrate female philopatry and high home range overlap between related adult females (Singleton

and van Schaik 2002; Knott et al. 2008; Morrogh-Bernard et al. 2010; van Noordwijk et al. 2012; Arora et al. 2012), and assume that young females generally settle into ranges that overlap highly with their female maternal relatives. More specifically, Morrogh-Bernard (2009) proposed the 'Petal Hypothesis' for explaining the spatial patterning of related females' home ranges: daughters settle into ranges that partially overlap those of their mothers, thus forming 'petals' around the mother's range which makes up the 'floral head'. She suggested that habitat resource distribution influences the extent of related females' home range overlap, with more homogenous habitats leading to smaller, less overlapping home ranges (Morrogh-Bernard 2009).

Our study aims to better understand the process of females' home range establishment among a population of Bornean orangutans (*P. p. wurmbii*). Using detailed longitudinal data, we address the questions of *how* and *where* young female orangutans establish their home ranges. Specifically, we investigate *how* a young female establishes her home range by quantifying 1) evidence of an 'exploration phase' among young females based on changes in their daily travel and home range size, 2) changes in young females' association patterns with their mothers, other adult female relatives, and unrelated adult females, and 3) changes in young females' association patterns with adult males, as well as potential social and spatial correlates of associations with males pre-parity. We investigate *where* a young female established her home range by quantifying 1) changes in home range overlap and shift between young females and both their mothers and their natal ranges, and 2) changes in the degree of home range overlap between young females and their mothers compared to the degree of home range overlap between young females and other related and unrelated adult females. By combining analyses of how and where a young female establishes her home range, we gain a better understanding of the mechanisms of female philopatry among orangutans.

METHODS

Study site and subjects

We conducted this study at the Tuanan Orangutan Research Station (2.151° S; 114.374° E) in the Mawas Reserve, Central Kalimantan, Indonesia, between 2003 and 2017. The study area is composed of approximately 12 km^2 of a gridded trail system through a generally homogenous, formerly selectively logged, peat-swamp forest. Orangutan density in the study area was approximately 4.25-4.5 individuals/km^2, the highest of any naturally occurring Bornean orangutan population (van Schaik et al. 2005).

Our primary study subjects were four nulli/primiparous females. Three of these females had been followed since the study began in 2003, and the fourth, since her birth in 2008. These four daughters are members of the same matriline, which spans 3 generations of maternally-related females (Fig. 2.1a). The females of this matriline all live in overlapping home ranges that are entirely encompassed within the Tuanan study area. In order to remain consistent and clear, we will use the term "daughters" to refer to these females – even after these daughters have become mothers themselves.

Our secondary study subjects included the three multiparous mothers of these daughters. Our tertiary study subjects were seven other local adult females (i.e. parous females) who are not related to the focal females (genetic relatedness established: see Arora et al. 2012 and van Noordwijk et al. 2012). From the perspective of

each daughter, there are three categories of adult female included in this study: her mother, her adult female relatives (all other parous females of her matriline aside from her mother), and the unrelated females.

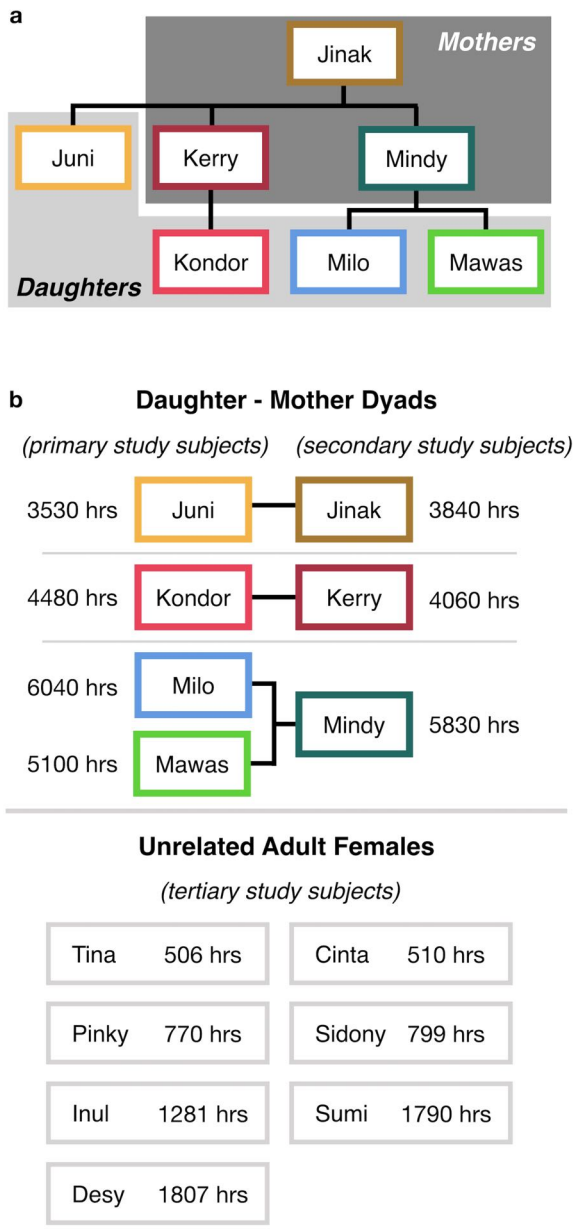


Figure 2.1: (a) The pedigree of daughters (primary study subjects) and mothers (secondary study subjects), and (b) the IDs and overall focal observation hours included in this study for all daughters, mothers, and unrelated females

Data collection

All data were collected in accordance with standardized protocols (https://www.aim.uzh.ch/de/research/orangutannetwork.html). Orangutans were found opportunistically, and then focal followed from morning nest until night nest for up to 10 days in a row (Altmann 1974). Figure 2.1b gives the total sample sizes per individual (in hours of focal observation). Our study includes focal association and social interaction data of the four daughters, but only focal location data for the other related and unrelated adult females. It was not possible to record data blind because our study involved focal animals in the field.

Focal behavioral data, including activity and distance to conspecifics, were recorded instantaneously at 2-minute intervals. Orangutans were considered "in association" if they were estimated to be within 50 meters of each other. The duration of time that focal females spent in association with specific age-sex classes of conspecifics or specific individual orangutans was calculated as the number of minutes (i.e. 2 x the number of 2-minute instantaneous intervals) spent in association. Daily proportions of time in association were calculated as the number of minutes in association divided by the total duration of the active period of the focal orangutan (in minutes).

All occurrences of agonistic social interactions between females were recorded continuously throughout all focal daughter follows. Agonistic social interactions included aggression, such as hitting, chasing, and biting, as well as clear displacements and instances of avoidance or fleeing. We recorded time, actor(s)/winner(s) and receiver(s)/loser(s) of the agonistic interaction, other orangutans also in association, and a description of each event.

The locations of the focal orangutans were collected at every night nest, and throughout the follow at 30-minute intervals. During the earlier years of the study, location data were collected by hand-drawn points on printed maps of the study area and trail system, whereas since 2012, waypoints were collected on hand-held GPS units. Garmin MapSource (v6) and ESRI's ArgGIS (v9.3) software were all used to digitize hand drawn maps and to import GPS unit data. Prior to all analyses, we applied a smoothing algorithm to the points in order to minimize GPS and observer movement error. A detailed description of this algorithm is given in Supplementary Methods 1.

Furthermore, habitat fruit availability data were collected from approximately 1500 marked trees in delineated plots within the study area. Fruiting data were collected once each month, and the percentage of stems bearing fruit was used as the measure of 'fruit availability' in our analyses (for details of fruit availability data collection methods, see (Vogel et al. 2016).

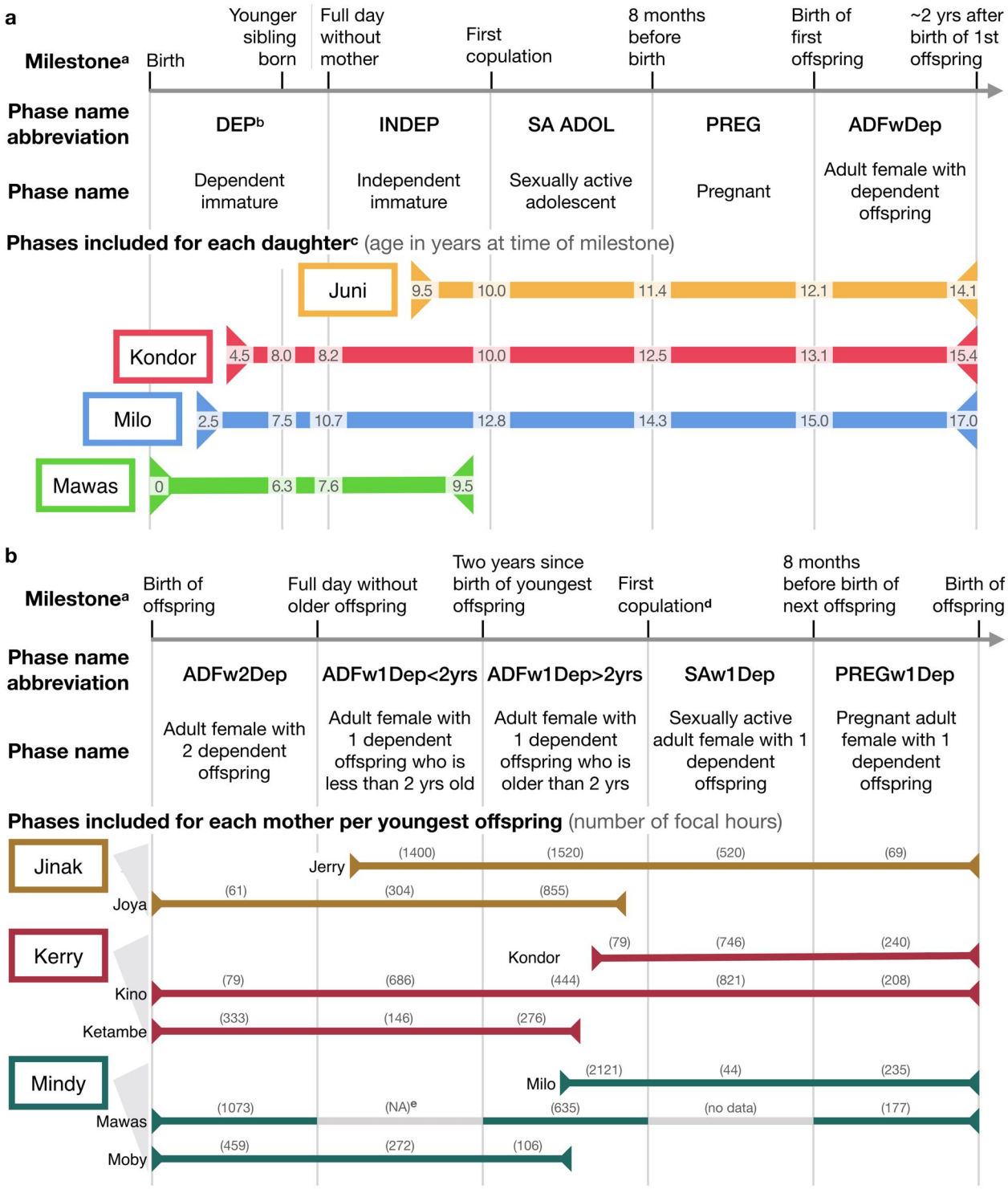
Data Analysis

Data sub-setting

For the majority of the analyses, all data were divided into *phases* based on key developmental or reproductive milestones of the *daughters*. Figure 2.2a describes these phases, gives the phase name abbreviations which are used in this text, and outlines the parameters used to delineate each different phase – i.e. which behavioral or reproductive milestone was used to determine the transition date between each phase. Table 2.S1 gives a more detailed overview of the daughters' phases, and the data included in these analyses. Furthermore, for each daughter and for each of her phases, we calculated the *mean fruit availability* as the mean of the fruit availability values for all months whose 15th day fell within that phase.

For one small subsection of the analysis, which focuses on mothers' movement and ranges, mothers' data were divided into *her own (rather than her daughter's) phases*, based on her own reproductive status and the dependence status of each of her offspring. Figure 2.2b describes these phases, gives the phase name abbreviations which are used in this text, and outlines the parameters used to delineate each different phase, and

the sample sizes therein. The mean fruit availability was also calculated for each of the mothers' phases, in the same way as for the daughters (above).



[a] New phase begins on day that milestone is first observed

[b] For daughters' day journey length and association with males analyses, only data after the mother's next offspring (i.e. the daughter's younger sibling) was born is included in the DEP phase

[c] Numbers on each bar represent the (estimated) ages of the daughter at time of milestone. Details about the dates, ages, durations, and sample sizes of daughters' phases are in Table S1

[d] First time that the mother is observed copulating with an adult male and within 1 year she is either pregnant, or she is observed copulating again (i.e. single isolated copulations, long before she actually becomes pregnant again, and without any subsequent copulations observed within 1 year, are ignored)

[e] Milo (older sibling) was not independent until Mawas was over 2 years old.

Figure 2.2: An overview of the phases into which the data were split: (a) phases of the four daughters, which were used for all analyses and by which all other females' data were divided, and (b) phases of the three mothers, which were used only for the analysis of mothers' daily travel and phase range size

Spatial data calculations

To measure daily travel, we calculated day journey length (DJL) for each of all of the daughters' and the mothers' nest-to-nest focal follows by summing up the cumulative Euclidian step distances between the focal orangutan's morning nest point, consecutive 30-minute range points, and the night nest point.

For each daughter and for each mother, we calculated a home range for each of her own phases. Furthermore, for each of all daughters' phases, we also calculated a home range for her mother, and for each other related and unrelated adult female. These home ranges are henceforth referred to as *phase ranges.* Phase ranges were delineated at the 95% isopleth of the kernel density utilization distribution (UD). To calculate the h (smoothing) value, we ran multiple iterations of the kernel density utilization distribution calculations for each phase range using progressively smaller and smaller h-values, and then calculated the 95% isopleth polygons for all of these UDs. We selected the UD with the smallest h-value (i.e. the least amount of smoothing, or estimation error) that still maintained a single polygon at the 95% isopleth (Fieberg and Börger 2012; R code modified after L. Börger and G. Cozzi). Only phase ranges which were calculated from at least 500 location points were included in the analysis, as this was the number of points required for a phase range to reach a stable size (more details are given in Supplementary Methods 2). We opted to focus our analyses on phase range outlines, rather than the encompassed utilization distributions. Because our field methods yielded short bouts (1-10 days) of high-resolution location data followed by periods of up to 6 months of 'missing' (i.e. no) data for each female, and because these data were further subdivided by phase, the overall shape and location of these ranges was less subject to the biases of our sampling methods, and therefore more reliable, than the utilization distribution therein.

Phase range centroid coordinates were calculated as the geometric center of mass of each range polygon, assuming uniform density. Phase range overlap values were calculated using the simple measure of the proportion of one animal's range that is overlapped by another animal's range. These calculations gave two directional values: the proportion of individual A's range overlapped by individual B's, and the proportion of individuals B's range overlapped by A's. Depending on the analysis (see below), we used either these singular directional overlap values, or dyadic overlap values. The dyadic overlap value between two individuals' concurrent ranges was calculated as the product of these two singular directional overlap values:

$$DyadicOverlap_{AB} = \frac{Overlap_{AB}}{Area_A} * \frac{Overlap_{AB}}{Area_B}$$

where $Overlap_{AB}$ is the area of overlap of the phase ranges of individuals A and B, $Area_A$ is the total range size of individual A and $Area_B$ is the total range size of individual B. Assuming that both animals used their ranges uniformly, this value gave a probability of both individual A and B being in the overlapping area simultaneously (Hutchinson and Waser 2007).

Statistical analysis

All spatial and statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). Phase range polygons, areas, and overlap, were calculated using the adehabitatHR packages (Calenge 2006). All general linear mixed models (LMMs) were calculated using the lme function from the nlme package (Pinheiro et al. 2018). Generalized linear mixed models (GLMMs) were calculated using the glmmTMB function from the glmmTMB package

(Brooks et al. 2017), except for those requiring the inclusion of a temporal autocorrelation variance structure and were therefore calculated using the glmmPQL function from the MASS package (Venables and Ripley 2002). In all applicable models, the focal's *phase* was included as a fixed effect and was coded as a polynomial contrast in order to test for patterns of change in the outcome variable over the course of time. Planned contrasts were also set for the *relationship* factor, in all applicable models, specifically: mothers compared to non-relatives, and mothers compared to other relatives. Single term deletions from each mixed model were performed using the drop1 function in the lme4 package (Bates et al. 2015), in order to obtain the likelihood ratio values for each fixed effect. Table 2.S3 gives details about the specific models used in each analysis, including outcome variables, fixed effects, and random effects.

To investigate *how* a young female establishes her home range, we first analyzed changes in daughters' and mothers' daily travel, specifically their day journey lengths (DJLs), and phase range sizes. Thus, two parallel analyses were conducted, one for daughters (i.e. nulli/primiparous females) and one for mothers (i.e. multiparous females), in order to establish what aspects of movement and range size changes could be attributed simply to reproductive phase, and what aspects were specific to young females' development. (Note that for all subsequent analyses, we used only data subdivided by daughters' phases.)

Next, we analyzed changes in the amount of time that daughters spent in association with their mothers through the daughters' phases. We then investigated overall changes in association time that daughters spent with their mothers and with other related and unrelated adult females over time, by calculating the proportion of time that each daughter spent in association with each other local adult female during each phase. Thus, for each focal daughter, for each of her phases, the total proportion of time spent in association with her mother, and with each other adult female in the area (including relatives and non-relatives) was calculated. Only association values for females with whom the focal daughter had non-zero phase range overlap during at least one phase (or – in cases where there was not enough focal data of the other female for her ranges to be calculated – non-zero proportion of time spent in association during at least one phase), were included in the analysis (i.e. adult females with whom the daughter never had any range overlap nor association were not included). In order to establish the phase at which the amount of time that daughters spent in association with their mothers no longer differed with the amount of time that daughters spent in association with other adult females (if at all), we ran four post-hoc tests (one for each phase except PREG, for which the sample size was too small).

Lastly, to investigate the effect of association with males on daughters' phase range development, we first looked at basic overall association time with flanged and unflanged males (these are different sexually mature male morphs; e.g. Utami Atmoko and van Hooff 2004; Dunkel et al. 2013) across the phases, including post-hoc per-phase tests designed to establish exactly how the time that daughters spent associating with flanged and unflanged males changed over the phases. We then looked at the effects of associating with males on daughters' association time with other adult females during the INDEP, SA ADOL, and PREG phases. Next, to specifically investigate the effects of male association on agonistic interactions between nulliparous females and other adult females, we calculated the rates of agonistic interactions involving daughters per hour of observation when she was in association and not in association with an adult male. Because agonistic interactions were rare, we pooled all social interaction data from the INDEP, SA ADOL, and PREG phases (i.e. from independence to first parturition) and only included the three daughters for whom we had data for all of these three phases. Interactions were

divided into those *directed towards the daughters by adult females,* and those *directed towards adult females by the daughters*. We compared the rates of both kinds of agonistic interactions when the daughter was in association with a male vs when she was not in association with a male. Lastly, to specifically investigate the effect of association with males on spatial exploration, we focussed on the three daughters who had already completed the SA ADOL phase. For each of these three daughters, we overlaid all of her location points from the SA ADOL phase over her INDEP range to see where she associated with males while sexually active, relative to her past range, and we tested whether being in association with a male was a predictor of whether a sexually active adolescent female was inside or outside her INDEP phase range.

To investigate *where* a young female established her home range, we quantified their shifting of ranges through daughters' development in two ways – in both cases, using the daughters' DEP phase ranges to represent the "natal ranges": 1) we compared both daughters' and mothers' phase range overlap of daughters' post-dependence phases to the daughters' natal range, and 2) we compared both daughters' and mothers' phase range centroid positions during daughters' post-dependence phases to the centroid of the daughters' natal ranges. We also investigated changes in the relative positions of mother and daughter phase ranges through daughters' phases in two ways: 1) we analyzed changes in the degree of daughter-mother phase range overlap, and 2) we measured the Euclidian distance between the centroids of daughters and their mothers through each of their phases.

Furthermore, we investigated changes in phase range overlap between daughters and mothers compared to the overlap between daughters and other related and unrelated adult females in the area. Only ranges based on at least 500 location points, and ranges of females with whom the focal daughter had non-zero proportion overlap during at least one phase, were included in the analysis. In order to establish the phase at which dyadic overlap between daughters and mothers no longer differed with dyadic overlap between daughters and other adult females (if at all), we ran four post-hoc tests (one for each phase except PREG, for which the sample size was too small).

RESULTS

Daily travel and phase range size

The mean day journey length (DJL) of daughters was 882 meters (range = 147 to 2550 m, SD = 425.2, n = 688). Daughters had significantly longer DJLs (square root transformed to ensure normality of the residuals) on days when they spent a lower proportion of time alone ($X^2(1) = 9.33$, $p < 0.005$; $b \pm SE$ = -2.34 ± 0.744, t = -3.14, $p < 0.005$), a higher proportion of time on the ground ($X^2(1) = 5.88$, $p < 0.05$; $b \pm SE$ =10.70 ± 4.417, t = 2.42, $p < 0.05$), and when fruit availability was higher ($X^2(1) = 68.87$, $p < 0.0001$; $b \pm SE$ =0.86 ± 0.101, t = 8.52, $p < 0.0001$). Phase had a significant quartic effect on DJL ($X^2(4) = 40.93$, $p < 0.0001$; $b \pm SE$ = 1.51 ± 0.591 , t = 2.56, $p < 0.05$) (Fig. 2.3a). The mean (across individuals) model predictions per phase – when holding other fixed effects constant at their means – indicated that DJLs increased from DEP to INDEP, then increased again from INDEP to SA ADOL, and then decreased to PREG and increased again to ADFwDep (see Fig. 2.2a for phase abbreviations).

The mean DJL of mothers was 726 meters (range = 72 to 2176 m, SD = 361.4, n = 1294). Mothers had significantly longer DJLs (square root transformed to ensure normality of the residuals) on days when they spent a

lower proportion of time alone ($X^2(1) = 53.25$, $p < 0.0001$; $b \pm SE = -3.91 \pm 0.527$, $t = -7.41$, $p < 0.0001$) and when fruit availability was higher ($X^2(1) = 117.65$, $p < 0.0001$; $b \pm SE = 0.665 \pm 0.060$, $t = 11.13$, $p < 0.0001$), while the proportion of time that they spent on the ground did not have a significant effect on DJL ($X^2(1) = 2.89$, $p = 0.091$; $b \pm SE = 7.54 \pm 4.437$, $t = 1.698$, $p = 0.0897$). Phase had a significant quartic effect on DJL ($X^2(4) = 21.43$, $p < 0.0005$; $b \pm SE = 1.16 \pm 0.399$, $t = 2.91$, $p < 0.005$) (Fig. 2.3c). The mean (across individuals) model predictions per phase – when holding other fixed effects constant at their means – indicated that DJLs decreased from ADFw2Dep to ADF1Dep<2yrs, and then increased to ADF1Dep>2yrs, stayed almost constant to SAw1Dep, and then peaked slightly during PREGw1Dep. Comparing PREGw1Dep to ADFw2Dep (i.e. looping back from pre-birth to post-birth), there was a decrease in DJL (see Figure 2.2b for phase abbreviations).

The mean phase range size of daughters was 265 hectares (range = 92 to 460 ha, SD = 109.8, n = 15). Daughters' tended to have larger phase ranges when mean fruit availability was higher ($X^2(1) = 6.12$, $p < 0.05$; $b \pm SE = 29.86 \pm 13.944$, $t = 2.14$, $p = 0.0760$), and the effect of phase also approached significance ($X^2(4) = 9.41$, p = 0.0516). Phase had a quadratic effect on range size ($b \pm SE = -88.72 \pm 31.528$, $t = -2.81$, $p < 0.05$) (Fig. 2.3b). The mean (across individuals) model predictions per phase – when holding mean fruit availability constant – indicated that range size increased from DEP to INDEP, peaked during SA ADOL, and then decreased again during PREG and during ADFwDep.

The mean phase range size for mothers was 239 hectares (range = 100 to 430 ha, SD = 96.3, n = 16). Mothers' range size was not significantly predicted by phase ($X^2(1) = 1.733$, $p = 0.6297$) or mean fruit availability ($X^2(1) = 0.383$, $p = 0.5358$). Although the mean phase range size during sexual activity was higher than during the other phases, the mean model prediction – controlling for mean fruit availability – was not significantly higher (Fig. 2.3d).

These results indicate that there is a difference between the patterns of change in DJL and phase range size between nulli/primiparous females (daughters) and multiparous females (mothers). Most notably, while daughters' DJL peaks during sexual activity, mothers' DJL peaks during pregnancy, immediately prior to the birth of their next offspring. Furthermore, unlike daughters, mothers do not show any significant changes in phase range size through their reproductive phases – i.e. there is no expansion of their range size during sexual activity, nor a subsequent contraction in range size after the birth of their offspring.

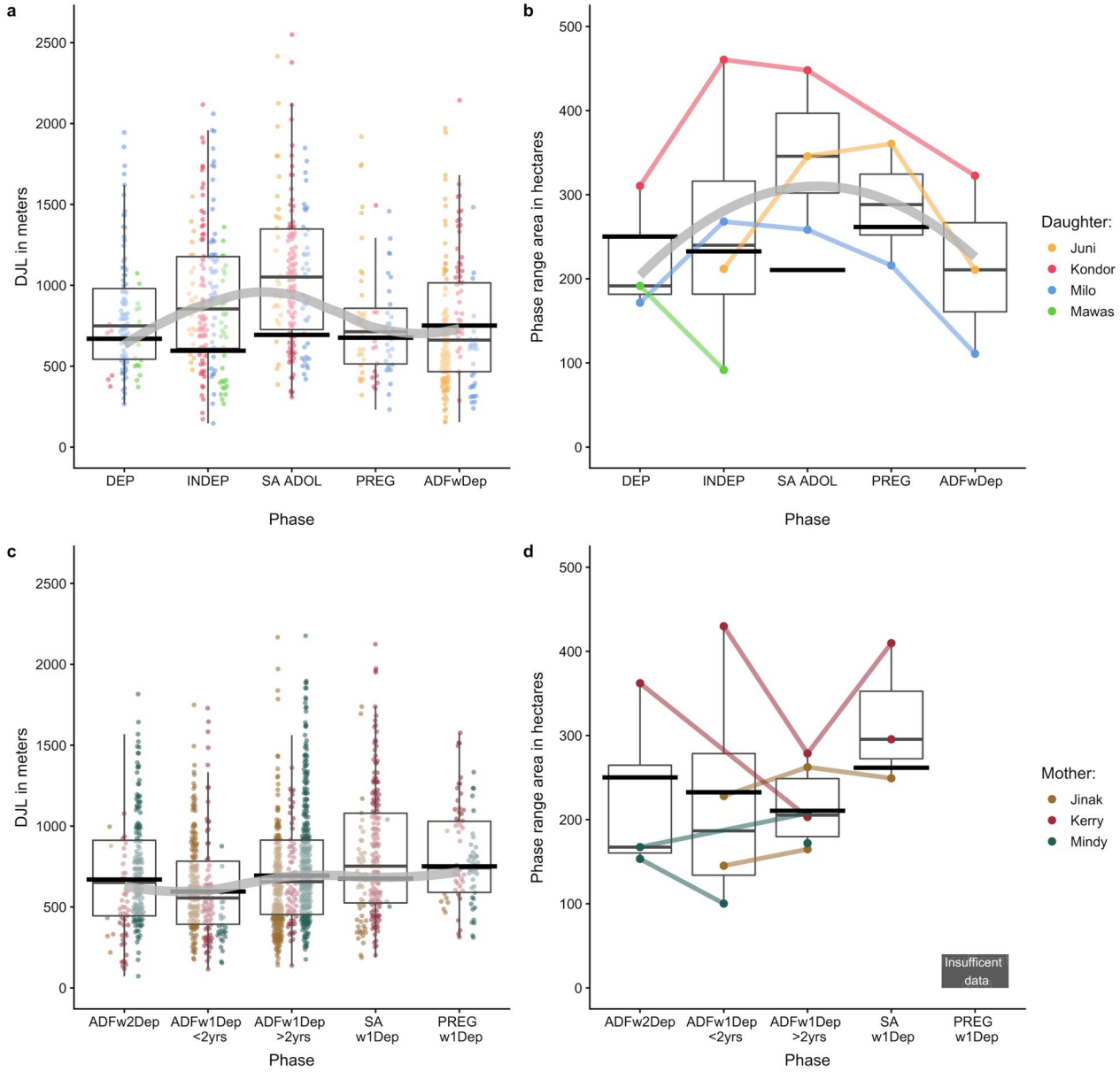


Figure 2.3: Daughters' (a) day journey length (DJL) and (b) phase range size results, and mother's (c) DJL and (d) phase range size results; points are raw data, boxes summarize the raw data, thick black horizontal lines represent mean model predictions when controlling for other factors, and the thick transparent grey lines represent the significant polynomial patterns seen across phases. Note that in the plot of mothers' phase range sizes (d), each line connecting points represents that mothers' phase range sizes with a particular youngest dependent offspring

Association with adult females

The proportion of time that daughters spent with mothers ranged from 0 to 0.994 (mean = 0.32, sd = 0.399, n = 16). The proportion of time that daughters spent in association with their mothers was significantly predicted by phase ($X^2(4) = 33.19$, $p < 0.0001$) but not by mean fruit availability ($X^2(1) = 0.067$, $p = 0.7956$). Their proportion of time in association decreased quadratically over the phases ($b \pm SE = 0.36 \pm 0.095$, $t = -3.81$, $p < 0.01$), with the highest association occurring during the DEP phase, followed by a 57% decrease into the INDEP phase, then

another 57 % decrease into the SA ADOL phase, and a further decrease down to a predicted value of no association during PREG, and a slight increase during the ADFwDep phase (Fig. 2.4a).

The proportion of time that daughters spent in association with other local adult females ranged from 0 to 0.994 (mean = 0.043, sd = 0.172, n = 129). The proportion of time that daughters spent with mothers is summarized above, while the proportion of time that they spent with relatives varied between 0 and 0.042 (mean = 0.007, sd = 0.012, n = 53), and that with non-relatives varied between 0 and 0.006 (mean = 0.0005, sd = 0.001, n = 60).

Daughters' time spent in association with other adult females was significantly predicted by an interaction between her relationship with the other adult female and her phase ($X^2(8) = 248.24$, $p < 0.0001$), but not by mean fruit availability ($X^2(1) = 0.069$, $p = 0.7923$). Post-hoc per-phase generalized linear mixed models show that daughters spent significantly more time, through all phases, with their mothers than with other related adult females and more time with their mothers than with unrelated adult females (Fig. 2.4b, Table 2.S4). Post-hoc per-phase models also indicated that mean fruit availability may have had a positive effect on daughters' association with other adult females during the INDEP and ADFwDep phases.

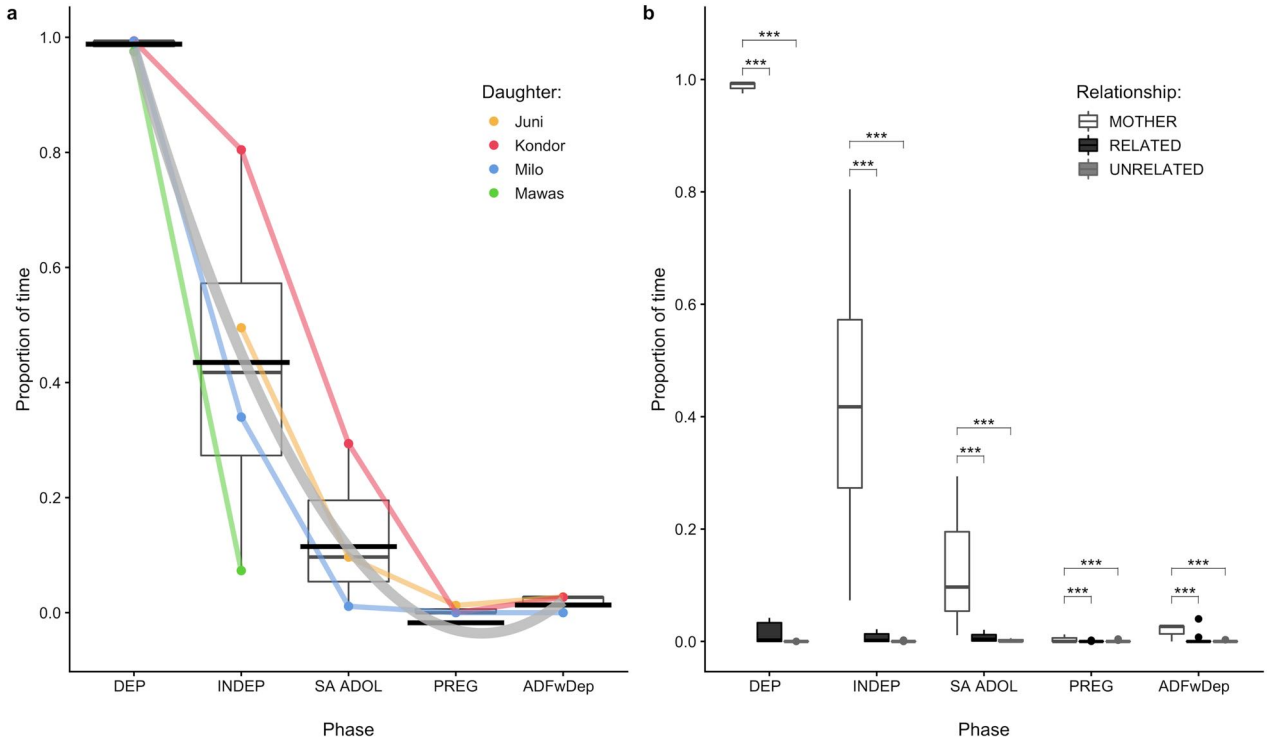


Figure 2.4: (a) Daughters' association time with their mothers, and (b) daughters' association time with each other adult female; in (a) points are raw data, boxes summarize the raw data, thick black horizontal lines represent mean model predictions when controlling for other factors, and the thick transparent grey lines represent the significant polynomial pattern seen across phases, in (b) significance starts refer to post-hoc per-phase tests of mothers compared to related females and mothers compared to unrelated females

Association with males

The proportion of time during each phase daughters spent in association with adult males (flanged or unflanged) varied between 0 and 0.267 (mean = 0.059, sd = 0.090, n = 16). The proportion of time that daughters spent in association with adult males has a clear peak during SA ADOL, when they spent approximately 45% of their time in association with an adult male. Daughters' proportion of time spent with adult males was significantly predicted by an interaction between adult male morph and her phase ($X^2(4) = 89.45$, $p < 0.0001$), but not by mean fruit availability ($X^2(1) = 0.135$, $p = 0.7136$). Post-hoc per-phase Poisson GLMMs show that daughters spent significantly more time with unflanged males than with flanged males during all phases, except for PREG when there was no difference (Fig. 2.5, Table 2.S5). The strongest difference was during INDEP and SA ADOL, when daughters spent almost 10 times more time with unflanged males than with flanged males.

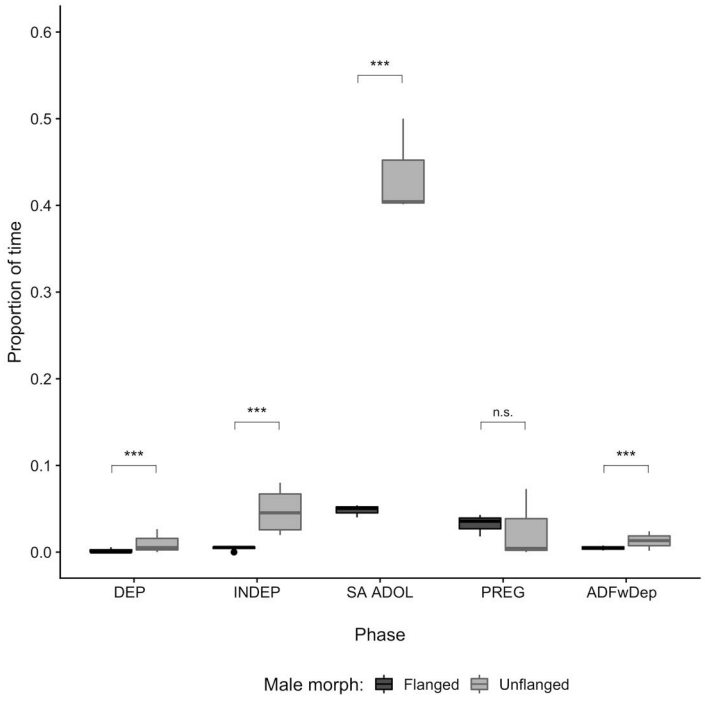


Figure 2.5: Daughters' proportion of time spent in association with each morph of adult male; significance starts refer to post-hoc per-phase tests of time spent with unflanged males compared to flanged males

From INDEP to PREG, the proportion of the day that a daughter spent in association with other adult females (including her mother) was not predicted by whether or not she was in association with an adult male (flanged or unflanged) that day ($X^2(1) = 0.009$, $p = 0.9238$). In other words, daughters were equally likely to associate with other adult females whether or not they were in association with an adult male as well.

During these same phases, daughters were aggressed by other adult females a mean of 0.025 times (sd = 0.015) per observation hour when they were not in association with an adult male, and 0.007 (sd = 0.0009) when they were in association with a male. Two out of three daughters received substantially lower rates of agonistic interactions from other adult females when in association with males (Fig. 2.6a). For the third, Milo, there was basically no difference, but she already received extremely low rates of agonistic interactions when not with an adult male. The only daughter who ever won agonistic interactions with other adult females, Juni, won a higher rate of agonistic interactions when in association with an adult male (Fig. 2.6b).

During her SA ADOL phase, association with a male was not a significant predictor of whether a daughter was inside or outside her previous phase's (INDEP) range ($b \pm SE = 0.206 \pm 0.149$, $t = 1.381$, $p = 0.1672$). In other words, sexually active daughters were equally likely to be with a male inside and outside in new and familiar areas.

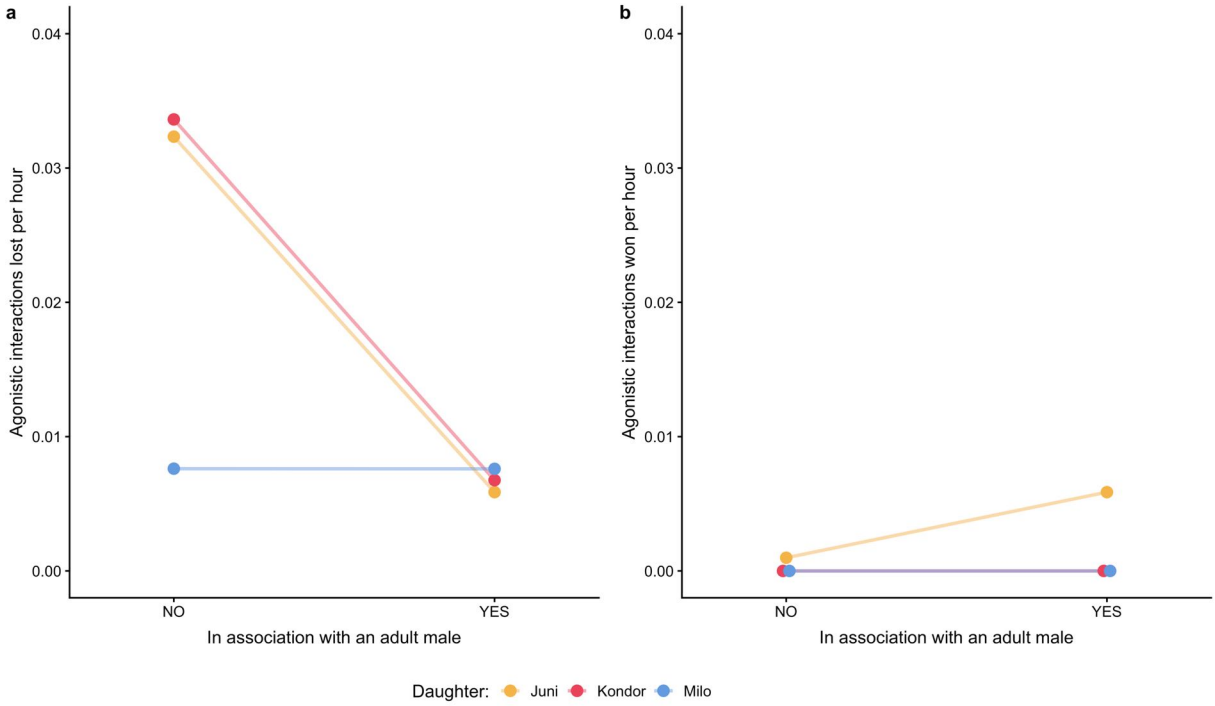


Figure 2.6: The rate (events per hour) of agonistic interactions that daughters (a) received from, and (b) directed towards, other adult females when in association and when not in association with an adult male

Phase range overlap and shift

Both mothers and daughters of each dyad maintained a substantial degree of overlap with the daughter's natal range throughout the four post-dependence phases (mean = 0.69, range = 0.53 to 0.90, SD = 0.098, n = 15). There were no significant changes in overlap through the phases ($X^2(3) = 0.269$, $p = 0.9658$), and mothers and daughters did not significantly differ in their degree of overlap with the natal range ($X^2(1) = 0.063$, $p = 0.8012$) (Fig. 2.S4a).

After daughters' DEP phases, both mothers and daughters shifted the centroids of their ranges away from the centroid of the daughter's natal range (mothers: mean = 374 meters, range = 170 to 594 m, SD = 139, n = 7; daughters: mean = 255 meters, range = 94 to 330 m, SD = 81, n = 8). The effect of phase on shift distance approached significance as a linear effect ($X^2(3) = 6.99$, $p = 0.0722$; $b \pm SE = 95.96 \pm 44.59$, $t = 2.15$, $p = 0.0636$), driven by the significant effect of class: mothers shifted the centroid of their ranges significantly farther from the natal range than daughters ($X^2(1) = 6.84$, $p < 0.01$; $b \pm SE = 111.88 \pm 45.19$, $t = 2.48$, $p < 0.05$) (Fig. 2.S4b).

Dyadic overlap between mothers and daughters varied between 0.13 and 0.98 (mean = 0.56, SD = 0.29, n = 14). Dyadic overlap was significantly predicted by phase ($X^2(4) = 40.69$, $p < 0.0001$) and mean fruit availability ($X^2(1)$

= 5.318, $p < 0.05$). Mean fruit availability had a significant positive effect on dyadic overlap value ($b \pm SE = 0.18 \pm 0.080$, $Z = 2.23$, $p < 0.05$). Dyadic overlap decreased quadratically over the phases ($b \pm SE = 1.44 \pm 0.189$, $Z = 7.63$, $p < 0.0001$), with the highest overlap occurring during the DEP phase (mean = 0.96, n = 3), and decreasing until it levelled off during the PREG (mean = 0.28, n = 1) and ADFwDep (mean = 0.29, n = 3) phases (Fig. 2.7a).

Distances between daughters' and their mothers' phase range centroids varied between 3 and 911 meters (mean = 282 m, SD = 263, n = 14). Distance was significantly predicted by phase ($X^2(4) = 15.32$, $p < 0.005$) but not by mean fruit availability ($X^2(1) = 0.789$, $p = 0.374$). Distance increased linearly over the phases ($b \pm SE = 404.86 \pm 106.20$, $t = 3.812$, $p < 0.05$), with the least distance occurring during the DEP phase (mean = 10 m, n = 3), and the largest distance during the ADFwDep phase (mean = 596 m, n = 3) (Fig. 2.7b).

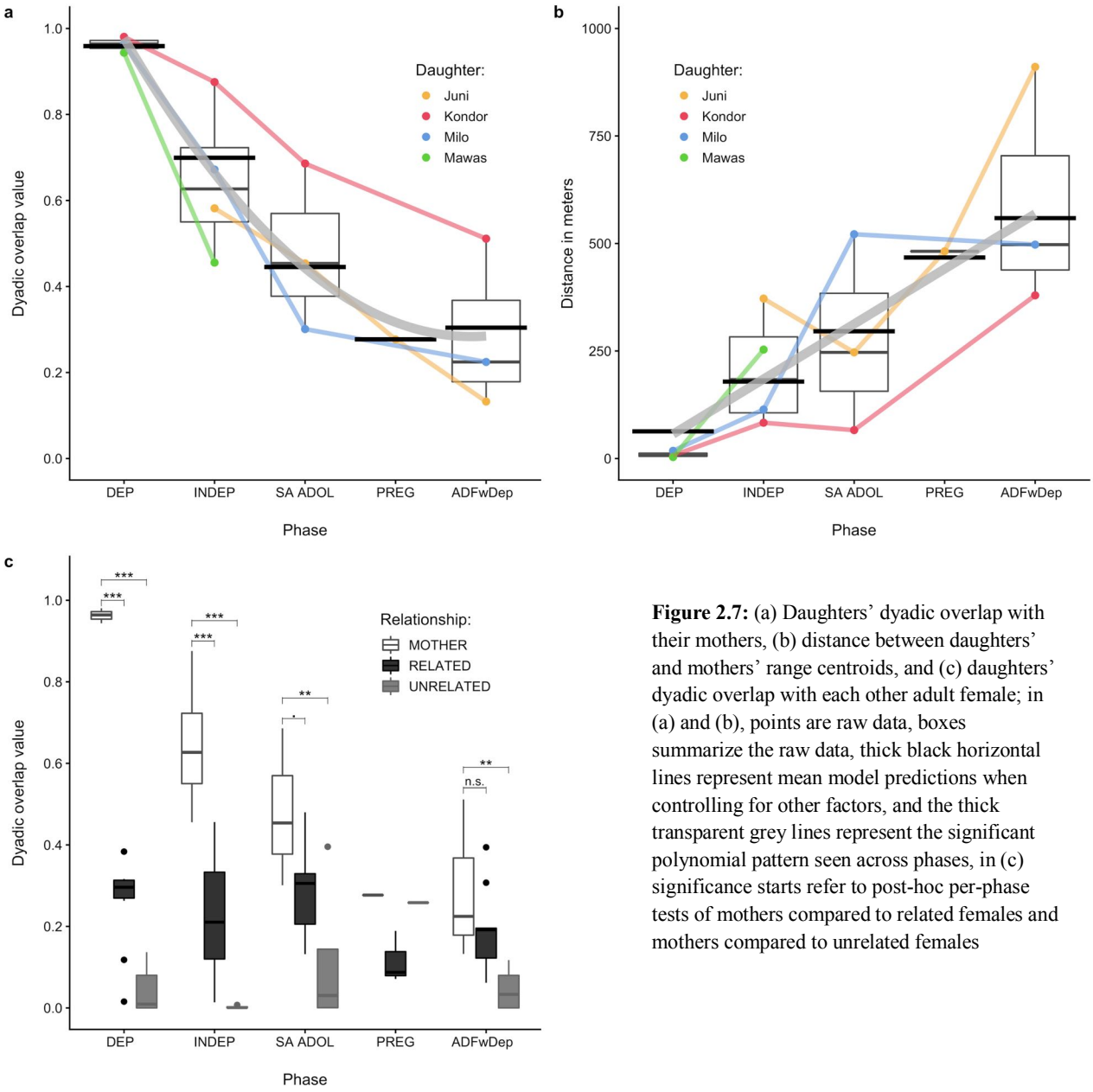


Figure 2.7: (a) Daughters' dyadic overlap with their mothers, (b) distance between daughters' and mothers' range centroids, and (c) daughters' dyadic overlap with each other adult female; in (a) and (b), points are raw data, boxes summarize the raw data, thick black horizontal lines represent mean model predictions when controlling for other factors, and the thick transparent grey lines represent the significant polynomial pattern seen across phases, in (c) significance starts refer to post-hoc per-phase tests of mothers compared to related females and mothers compared to unrelated females

The dyadic overlap index between daughters and other individual local adult females ranged from 0 to 0.981 (mean = 0.24, sd = 0.23, n = 79). The dyadic overlap between daughters and mothers was summarized above, while the dyadic overlap between daughters and their adult female relatives ranged from 0.01 to 0.48 (mean = 0.23, sd = 0.12, n = 43), and dyadic overlap with non-relatives ranged from 0 to 0.40 (mean = 0.059, sd = 0.10, n = 22). Figure 2.S5 shows maps of all daughters' and surrounding adult females' ranges per phase.

Daughters' dyadic overlap with other adult females was significantly predicted by an interaction between her relationship with the other adult female and her phase ($X^2(8) = 53.78$, $p < 0.0001$), as well as by the mean fruit availability during that phase ($X^2(1) = 5.50$, $p < 0.05$). Post-hoc per-phase linear mixed models show that 1) daughters had significantly higher overlap with their mothers than with unrelated females through all phases, and 2) daughter had significantly higher overlap with their mothers than with related females during the DEP and INDEP phases, but from the SA ADOL on the daughters' overlap with their mothers began to approach that with other adult females, and by their ADFwDep phase, daughters overlap with their mothers was no longer significantly different from that with other related adult females (Fig. 2.7c, Table 2.S6). Mean fruit availability was positively correlated with dyadic overlap between daughters and other adult females in the overall model ($b \pm SE = 0.028 \pm 0.012$, $t = 2.35$, $p < 0.05$), but this significant effect was lost in the post-hoc per-phase models.

DISCUSSION

We conducted a detailed longitudinal study of female movement and association patterns before and after their first parturition in order to gain a better understanding of the process of home range establishment among wild female Bornean orangutans at Tuanan. We found that after the birth of her younger sibling, while she is an independent immature (INDEP), a young female begins to widely explore her surroundings, increasing the size of her home range and the length of her daily paths, suggesting that this is a time of increased spatial exploration. This exploration continues through her adolescence (SA ADOL), a time during which female orangutans are sexually active but not yet able to conceive. During this time, she associates more with unflanged than with flanged males. She may receive fewer agonistic interactions from other adult females when in the presences of an adult male, but she does not specifically use this 'protection' to move through previously unfamiliar areas. A young female and her mother maintain a high degree of overlap with her natal range, but gradually decrease their degree of overlap with each other, as they shift their ranges away from each other's. By the time she is a sexually active adolescent (SA ADOL), a young female and her mother share as much overlap as she does with other related adult females, although she continues to associate more with her mother than with other related adult females, and still does so after the birth of her first offspring. After the birth of her first offspring (ADFwDep), a young female ends up living in a range that has a high degree of overlap with her original natal range and also includes some new surrounding area. Mothers of these daughters also maintain a high degree of overlap with their daughters' natal range, however the center of their ranges shift farther from the daughter's natal range, indicating that they are also incorporating some new areas into their ranges.

Mechanisms of home range establishment

Our results show that range size and day journey length (DJL) both peak during adolescent sexual activity, suggesting that young females go through an 'exploration phase' during which they move widely, outside their natal ranges. This is consistent with previous studies that have noted sexually active females' increased home

range sizes and day journey lengths, and/or the frequency of observations of adolescent females in areas previously not included in their ranges, suggesting expanded home ranges (ex. Galdikas 1995; Singleton and van Schaik 2001; Wartmann et al. 2010). However, it is interesting to note that the largest degree of increase in both range size and day journey length occurred immediately post-dependence: The clear increases in range area and day journey length from when a young female is dependent on her mother to when she is an independent immature indicate that young females begin to explore their surroundings more widely as soon as some degree of spatial independence is achieved, and prior to the onset of sexual activity. Although home range expansion during sexual activity / mating seasons has been documented among some species of bears (Dahle and Swenson 2003b; Edwards et al. 2013), we are unaware of studies of other taxa which separate nulliparous and multiparous sexual activity, and/or pre- and post-onset of adolescent sexual activity phases (if applicable – such a differentiation does not apply to all species).

An important question is whether the changes that we see in DJLs among nulli/primiparous females are simply the result of reproductive status – and therefore seen also among multiparous females - or if they are unique to these young females. Our results suggest that nulli/primiparous females have a different pattern of DJL increase and decrease than the pattern in multiparous females. First of all, nulli/primiparous females have, overall, longer DJLs (and larger home ranges) than multiparous females, the only exception being when the young females are still dependent and travelling with their mothers. Thus, the presence of dependent offspring shortens DJLs (see also Wartmann et al. 2010), which is consistent with differences observed between subadult and adult female chimpanzees (Pontzer and Wrangham 2006). It is likely that, overall, the presence of an infant – either clinging and adding weight, or travelling independently and needing support and assistance - slows down mothers and limits the distance that they can travel in a day, as has been observed in other taxa (chimpanzees: Pontzer and Wrangham 2006; brown bears: Dahle and Swenson 2003a). It is also possible that body size differences between nulli/primiparous females and multiparous females contribute to their overall differences in DJL. Female orangutans do not reach their full adult size until sometime after the birth of their first offspring (Leigh and Shea 1995; C. Schuppli, SSUA, and MAvN, unpublished data), and canopy travel may be energetically less costly for these smaller females, allowing them to travel farther than larger, fully grown, multiparous females (Halsey et al. 2016).

More specifically, however, the pattern of DJL increases and decreases seen among the nulli/primiparous daughters was different from that observed among their multiparous mothers: nulliparous females have the strongest increase in DJL when they first become independent from their mothers, achieve their longest DJLs during sexual activity, and show a marked decline in DJL from sexual activity to pregnancy. Multiparous females, on the other hand, show a pattern of increasing DJL length that mirrors the growth trajectory of their dependent offspring: When they have two dependent offspring (a newborn and an older, soon-to-be-independent offspring), they have longer DJLs than after the older offspring first achieves independence. Subsequent to this, multiparous female's DJL increases slightly, phase by phase, as their single dependent offspring grows in age/size and is able to move faster and more independently, and also contributes to the faster depletion of feeding sources. Thus, their peak DJL is reached during pregnancy – when their dependent offspring is old enough to be causing some considerable feeding competition, but before they have another newborn to slow them down. In chimpanzees, females in estrus have longer DJLs that anestrous females (Matsumoto-Oda and Oda 1998; Bates and Byrne

2009), and sexually receptive mothers have faster travel speeds than mothers with offspring (Wrangham 2002). It would appear that, among orangutans, the reduction in DJL due to the presence of a dependent offspring outweighs the increase in DJL due to sexual receptivity. The difference with chimpanzees may be linked to the arboreal travel of orangutans, which is energetically more costly (Thorpe et al. 2007; Manduell et al. 2012), and also often requires that mothers assist or wait for their otherwise independently-moving offspring when crossing canopy gaps (van Noordwijk and van Schaik 2005; Chappell et al. 2015). Our results make clear that young females – from the time they are independent immatures until they become pregnant – experience an increase in daily travel and range size that suggests an 'exploration phase', which is unique to nulliparous females and not simply a reflection of sexual activity.

Sexually active nulliparous females spent more time in association with unflanged than flanged males. This is consistent with previous studies at other sites, which have noted that flanged males seem to have limited interest in nulliparous females, despite these young females' interest in them (Schürmann 1982, Galdikas 1995). Flanged male orangutans can almost always displace unflanged males (Schürmann 1982, Utami et al. 2002), suggesting that their lack of interest in nulliparous females opens the door for unflanged males to associate with these females. This is consistent with observations of East African chimpanzees, among whom males prefer older parous females over nulliparous females, and higher-ranking males will attempt to lower the access of lower ranking males to these multiparous females (Muller et al. 2006).

Male support during agonistic interactions between female orangutans has been previously documented among the Tuanan orangutans: Marzec et al. (2016) described an instance of coalitionary lethal aggression in which an adult female and her unflanged male consort attacked another adult female, who was eventually protected by a flanged male. Thus, males provided support to both the attacking female and her victim (Marzec et al. 2016). Nonetheless, the present study found only tentative support for the idea that adult males may provide nulliparous/adolescent females with social support against older, more established, resident females. It is true that two out of three focal nulliparous females in our study received lower rates of agonistic interactions from adult females when in association with a male (and the third female's rate was negligible to begin with), consistent with Kahlenberg et al.'s (2008) observation of chimpanzees. However, there was no evidence that associating with males allows these young females to explore new, unfamiliar areas, which could simply be because they hardly move away from their natal area to begin with. In other populations with different habitat ecology, less dense orangutan populations, and more unoccupied space, this social protection may operate, since young females may incorporate more unfamiliar areas into their home ranges as they mature. However, it would only allow exploration and not facilitate settlement, given that females spend most of the time alone and would still be vulnerable to being chased when encountering dominant resident females.

Resource availability has a significant inverse relationship with home range size among several species of bears, with females travelling farther and wider to obtain resources during periods of scarcity (Moyer et al. 2007; Edwards et al. 2013). Among female orangutans, we showed that temporal variation in habitat fruit availability had a variable effect on movement and ranges. Young females had longer DJLs, and – unlike their mothers – also larger ranges, when fruit availability was higher. This suggests that younger/nulliparous females may take advantage of increases in fruit availability in order to expand their ranges and spend more time within other adult females' home ranges. High fruit availability presumably facilitates exploration by nulliparous females: lessening

the degree of scramble competition among females, may allow them to range farther within the boundaries of already-established adult females' ranges, whereas for already-established adult females, this expansion is not necessary. However, it should be noted that specifically investigating the influence of fruit availability on female range size – for instance, by subdividing location data based on periods of high and low fruit availability, and comparing individuals' range sizes under these two conditions – is beyond the scope of this study. Thus, the full effect of habitat fruit availability fluctuations on female home ranges remains to be determined (Ashbury et al., in prep.).

Spatial correlates of home range establishment

The extreme conservatism in space-use among the female orangutans in Tuanan is notable: daughters maintained high spatial overlap with their mothers and other maternal kin, as well as overlap with their natal ranges, even after their first parturition. Mothers are sharing part of their home ranges with their maturing and fully adult daughters, and both (especially mothers) are incorporating some area outside of the daughter's natal range as well. It should be noted that these orangutans do live in an open system: sons from this same matriline leave the area (van Noordwijk et al. 2012), and many adult males come and go (Spillmann et al. 2017) – in other words, it is safe to assume that these females are not maintaining this exceptionally high life-long site-fidelity simply because they have nowhere to disperse to. Rather, it is likely that the costs which females would accrue if they were to disperse, such as delayed age at first reproduction, would far outweigh the potential benefits of dispersing.

The exceptionally high degree of lifetime site fidelity and home range overlap among adult females in the Tuanan study area is likely facilitated by the resource distribution, and may be necessitated by the high orangutan population density, of this area. Throughout the Tuanan forest, relatively high-quality food sources (fruiting trees and vines) are frequent, small, and homogenously distributed, and orangutans have relatively high daily caloric intake, even during periods of low fruit availability (Marshall et al. 2009, Vogel et al. 2015). These habitat factors lead to relatively relaxed scramble competition, and thus selection for spatial differentiation between adult females, especially related adult females, is also relaxed. Tuanan is also home to the highest recorded population density of wild Bornean orangutans, at approximately 4.25 – 4.5 individuals per km^2 (van Schaik et al. 2005). This high population density means that there are no "open areas" into which a young female could establish her home range; instead she must share range space with other adult females. Thus, the unique local ecology of the habitat and orangutan population at Tuanan means that females must, and can afford to, have highly overlapping home ranges (Vogel et al. 2015), very similar to the Sumatran swamp forest of Suaq Balimbing (Singleton and van Schaik 2001). Short-term mutual avoidance, especially during times of scarcity, may be enough to offset the competitive costs of this high range overlap. In less productive or more variable habitats with less abundant or lower-quality fallback foods, scramble competition may be more intense and open areas may be more available, and thus spatial differentiation between even-closely-related females may be more likely.

Morrogh-Bernard's (2009) Petal Hypothesis predicts that daughters will settle into home ranges that surround and overlap their mothers'. Specifically, this hypothesis predicts that in homogenous habitats (including Sabangau where this hypothesis was developed), female orangutans will have small home ranges, with more overlap between mother-daughter dyads than between other related individuals, while in heterogenous habitats, females will have larger home ranges and a high degree of overlap with all female relatives (Morrogh-Bernard 2009).

Although we did not directly test it, our results provide mixed support for this hypothesis in Tuanan: while we do see primiparous females settling into home ranges that surround and overlap with their mothers', and the relatively small home ranges that are predicted for a homogenous habitat, we don't see higher overlap between parous daughters and their mothers, than between parous daughters and other related females. Like Sabangau, Tuanan is a relatively homogenous peat swamp forest; however, Tuanan has significantly higher forest productivity and better overall orangutan diet quality, and thus a denser population (van Schaik et al. 2005; Vogel et al. 2015). We therefore suggest that habitat productivity and orangutan population density (as discussed above), may be a stronger driving force behind the spatial patterning of female orangutan home ranges than the degree of habitat heterogeneity *per se*.

Benefits and costs of philopatry

Many of the costs of dispersal among mammals are well documented, and include such disadvantages as reduced feeding efficiency (due to a lack of familiarity with the location of food sources and/or the techniques needed to acquire them), higher stress levels, delayed breeding and thus lower reproductive potential, and increased vulnerability to predators (Isbell and van Vuren 1996; Ronce 2007; Clutton-Brock and Lukas 2012; Walker et al. 2018). Female orangutans have very broad diets (Russon et al. 2009), which are learned over years by socially induced learning (Schuppli et al. 2016; Schuppli et al. 2017). High overlap with the natal range and exploration during times of high resource availability allow females to keep their diet, and not accrue costs of association with the risky exploration of novel food items to include in the diet (cf. Bastian et al. 2010).

Furthermore, dispersing females lose the potential benefits of associating with their kin, such as opportunities for their dependent offspring to play with 'safe' partners. Indeed, van Noordwijk et al. (2012) found that related females allowed their offspring to engage in social play while unrelated adult females tended to actively prevent their offspring from engaging in social play. Play is likely an important behavior for mammalian social and locomotor development (Byers and Walker 1995; Fairbanks 2000; van Leeuwen et al. 2013; Heintz et al. 2017), and because orangutans have single births, and do not live in cohesive social groups, there are limited opportunities for immatures to play, especially with peers (van Noordwijk et al. 2012; van Noordwijk et al. 2018). In general, unrelated adult females show low social tolerance to each other, even to the extent of a documented instance of lethal aggression between two unrelated adult females (Marzec et al. 2016). Thus, female philopatry – i.e. the spatial clustering of maternal relatives exhibiting high social tolerance – among orangutans is likely vital for the healthy social and locomotor development of their offspring.

The potential benefits of dispersal for female mammals include reduced competition for resources (assuming that dispersing individuals are able to move to an area with relatively more resources), escape from an area or group where there is a high risk of infanticide by immigrant males and/or predators, inbreeding avoidance, and avoidance of the indirect costs of resource competition with kin (Clutton-Brock and Lukas 2012). The first three of these do not directly apply to female orangutans at Tuanan; there is no evidence that surrounding areas have higher resources and lower population densities, unfamiliar males are found everywhere due to their predominantly nomadic ranging patterns (Spillman et al. 2017), predation on adult orangutans is very rare (Kanamori et al. 2012; Knott et al. 2019), and males' long-range natal dispersal is sufficient to prevent inbreeding (Nietlisbach et al. 2012). However, it is likely that philopatric female orangutans experience increased feeding

competition with their maternal kin. There is strong evidence that orangutans maintain their predominantly solitary lifestyle because their high energetic needs (due to their large body size and arboreal travel) cannot be readily met when they are in direct, longer-term, feeding competition with close-by conspecifics (Mitani et al. 1991; van Schaik 1999; Wich et al. 2009; Kunz et al. in prep.). Indeed, we found that females in association with other orangutans, and females with older dependent offspring, travel farther each day – this is likely in order to satisfy their caloric intake, as food patches are depleted significantly faster when visited by more than one individual. Thus, even with limited association, there are likely costs associated with indirect feeding competition among female orangutans with overlapping home ranges. However, in a saturated habitat, moving away would not reduce scramble competition, so the choice is between scramble competition with kin versus with non-kin, which makes no difference for inclusive fitness as long as the habitat remains saturated. Thus, the benefits of remaining in a familiar habitat and having social access to maternal relatives would tip the balance in favor of philopatry.

Overall, it is clear that, among female orangutans at Tuanan, the benefits of philopatry far outweigh the costs, and lifetime site-fidelity is exceptionally high (this study, van Noordwijk et al. 2012; Arora et al. 2012). It is likely that, to the extent allowed by local habitat ecologies and resource distributions, this is true for all orangutan populations. Our observations of female site-fidelity are also supported by genetic studies which have shown stable boundaries in mtDNA haplotypes in Sumatra (north versus south of lake Toba) and in Borneo (between major rivers) and significantly higher clustering and geographic differentiation of mitochondrial haplotypes than Y-chromosomal variation (Arora et al. 2010; Nietlisbach et al. 2012; Arora et al. 2012; Nater et al. 2013). Thus, our longitudinal behavioral evidence highlights important aspects of females' behavioral development through which this population structure is achieved: a spatial exploration phase prior to first parturition, high socio-spatial tolerance between maternal kin, and mothers sharing and shifting their ranges and thus accommodating their maturing daughters.

Implications for orangutan conservation

The implications of our results for orangutan conservation efforts are of particular importance. All orangutan species are classified as critically endangered by the IUCN (Ancrenaz et al. 2019). Our results highlight the extreme spatial conservatism of female orangutans – their long-term site-fidelity and maintenance of overlap with their mothers and other maternal relatives – as well as the importance of their social bonds with, especially, their mothers. These results therefore emphasize the potentially detrimental effects of any forest loss for female orangutans, while male orangutans may cross open space and/or make use of forest corridors to move between forest fragments or to escape from more to less disturbed areas, females may be less likely to do so. Thus, any loss of habitat in which female orangutans live could lead directly to the loss of those female orangutans. Females' high lifetime site-fidelity should therefore be taken into consideration by land-use planning initiatives.

Furthermore, it is estimated that approximately 1,250 wild-born orangutans are currently being cared for in rehabilitation facilities, where the ultimate goal is release back into wild habitats (Palmer 2018). Additionally, mature wild orangutans are increasingly being translocated from high risk areas (due to forest clearing, hunting, crop-raiding, etc.) into lower risk areas. In Indonesia, this translocation practice is carried out by the government, private companies, and NGOs, and is not strictly regulated. As such, it is difficult to estimate how frequently translocation occurs, however, some reports suggest that it is quite common (J. Sherman, Wildlife Impact,

personal communication). Our results indicate that the release of rehabilitant and translocated female orangutans into existing/established populations is likely to be stressful for both the incoming individuals and also to the last remaining natural and healthy populations. Incoming females will raise the population density and compete for resources, thus altering the balance of females' spatial patterning. We recommend rigorous long-term monitoring of reintroduced and translocated orangutans, to better understand the efficacy of these conservation efforts, as well as factors that may contribute to its success or failure.

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SUPPLEMENTARY MATERIALS

Significance Statement

The mechanisms of philopatry and the process of home range establishment among solitary animals with slow life histories are difficult to study and poorly understood for most species. We investigated this process among female Bornean orangutans, using a unique long-term data set comprising 15 years of social and spatial data. We analyzed changes in the ranging and association patterns of young female orangutans as they developed, matured, and became mothers. We found that females went through a post-dependence phase of exploration characterized by an increase in range size and day journey length, and then settled into home ranges that overlapped highly with their mothers and other female kin, though they associated preferentially with their mothers. Our results illuminate the extreme long-term site-fidelity of these female orangutans, and emphasize the ecological and social importance of female philopatry among orangutans.

Supplementary Methods

1: GPS smoothing algorithm

All location points used in these analyses were run through two error-smoothing algorithms prior to the spatial (DJL and phase range) calculations. The error-smoothing algorithms were designed to minimize location point error and thus inaccurate GPS fixes, and were especially important for the calculation of day journey lengths (DJL) (Fig. 2.S1).

It was clear to observers in the field, following focal orangutans, that there were two sources of GPS error: "imprecise stops" and "impossible jumps." *Imprecise stops* occurred when orangutans would stop moving (to rest or feed in one place) for multiple half hour intervals, and the points taken at each interval were not in the same location; step-lengths between location points could be as far as 60 meters despite the fact that the focal orangutan hadn't actually moved at all. This pseudo-movement was caused mostly by low satellite reception (GPS inaccuracy), but some could also be attributed to observer movement (as the observer – carrying the GPS unit – moved around to different observation points). Imprecise stops caused a non-random amount of error in DJLs: follows with shorter DJLs – i.e. those during which the orangutan had stopped more often – had higher levels of error, while follows with longer DJLs – i.e. more directional travel – had generally more accurate GPS fixes and less convoluted observer movement, and thus had lower margins of error. *Impossible jumps* were caused by complete losses in satellite coverage at the time that a point was made, resulting in a location point that was farther from the previous than it would be possible for an orangutan to have actually travelled in 30 minutes. Furthermore, impossible jumps were characterized by the fact that they generated a single point outlier, i.e. the point *after* the error point was closer to the point *preceding* the error point than to the error point itself. An impossible jump would add two huge step-lengths to a follow's DJL, in some cases as much as doubling the DJL of that follow.

We therefore developed two simple smoothing algorithms in order to minimize these two types of GPS error; one to minimize pseudo-movement during imprecise stops, and the other to eliminate huge steps caused by impossible

jumps. The points from each nest-to-nest focal follow were run through these two algorithms, one after the other, which adjusted point locations as necessary, according to a few simple rules.

Imprecise stops

This algorithm has 3 main steps, all based on a single concept: If at least 3 location points are within a certain radius, the *stationary threshold*, of each other, their locations should be averaged. Step 1 measures the distance from the first location point to the second, then from the first location point to the third, and so on, for as many points as the distance remains less than the stationary threshold. If at least 2 points are within the stationary threshold of the first, then all points within the stationary threshold, including the first point, are averaged. Step 2 does the same but in reverse, starting with the last point of the follow. Thus, it measures the distance from the last location point to the second-last location point, then from the last location point to the third-last location point, and so on, for as many points as the distance remains less than he stationary threshold. If at least 2 points are within the stationary threshold of the last, then all points within the stationary threshold, including the last point, are averaged. Step 3 applies the same rule as Step 1, and in the same way, but on a rolling basis through all points in the follow. So, one at a time, for each point, starting with the second point in the follow, the distance from the point-of-concern to the next point is measured, then from the point-of-concern to the *next* next point (2 points later), and so on (3 points later, 4 points later, etc), for as many points as the distance remains less than the stationary threshold. If at least 2 points are within the stationary threshold of the point-of-concern, then all points within the stationary threshold, including the point-of-concern, are averaged. If only one point, or no points, are within the stationary threshold of the point-of-concern, then the points are left as is. Either way, the algorithm then moves on to the next point, and begins again to measure the distance to subsequent points, and so on.

The stationary threshold was set at 10.4 meters and was chosen based on a simple analysis of distances between half-hour points while a focal orangutan rested in a nest. Continuous 2-minute interval behavioral observations indicating that a focal orangutan was resting in a day nest was the clearest way of establishing that a focal orangutan did not move at all. We therefore combed through all activity data and extracted time intervals ≥30 minutes during which a focal orangutan was recorded continuously as "resting in a nest." We then measured the step-lengths between consecutive location points taken during these times. This gave us a distribution of step-lengths that occurred when a focal was not moving – i.e. a distribution of pseudo-movement step-lengths. Through trial and error, and visual inspection of focal orangutan paths and their adjustments, we determined that using the 3rd quartile of this distribution as our stationary threshold yielded the best balance of error-smoothing without over-smoothing; in our case, this distance was 10.4 meters. Figure 2.S2a shows an example of a follow that has had multiple imprecise stops smoothed out of the GPS points.

We believe that using a general algorithm that includes a site-specific stationary threshold, allows for our GPS smoothing method to be applied to data collected at other sites. Using a site-specific stationary threshold is necessary to account for inter-site differences in satellite coverage, topography, forest cover, and other factors that affect the accuracy of GPS fixes.

Impossible jumps

This algorithm has 3 main steps, all based on a single concept: If a step-length between two consecutive points is greater that a certain distance, the *movement threshold*, then the outlying point causing this distance should be relocated back in line with the points before and/or after it. Step 1 checks if the distance between the first and second points of the follow is greater than the movement threshold, and, if so, the first point is moved to the same location as the second point. Step 2 checks if the distance between the last and the second-last points of the follow is greater than the movement threshold, and, if so, the last point is moved to the same location as the second-last point. Step 3 rolls through the second to second-last points in the follow and measures the distances between 1) the point-of-concern and the preceding point, and 2) the point-of-concern and the subsequent point. If both distances are greater than the movement threshold, then the point-of-concern is relocated to a position directly between the preceding and subsequent points. If neither, or only one, distance is greater than the movement threshold, then the points are left as is. Either way, the algorithm then moves on to the next point, and measures the preceding and subsequent distances, and so on.

The movement threshold was set at 600 meters and was chosen based on a simple investigation of all step-lengths between consecutive half-hour points in the data set. Plotting the distribution of all step-lengths yielded a left-skewed distribution with a long tail and several high outliers. We cross-checked these outliers with the behavioral data and found them all to be errors (i.e. there was no indication in the behavioral data that the orangutan was travelling remarkably fast/far). We then cross-checked the highest step-lengths in the distribution, working our way down, until we found a clear cut-off point: above 600 meters, longer step-lengths could not be explained by the behavioral data, whereas below 600 meters, step-lengths – many of which were still remarkably long for an orangutan – had clear behavioral correlates (for example, almost all 2-minute interval focal activities marked as "move", notes from observers about how quickly the focal was travelling, usually with some indication of why (being chased, moving quickly towards a long call, etc)). Figure 2.S2b shows an example of a follow that has had an impossible jump smoothed out of the GPS points.

2: Range size and Number of Location Points

In order to determine - and if necessary, account for - a relationship between the number of location points included and the size of a phase range (given our method of calculating range polygons), we conducted a simple analysis investigating changes in the size of a range with an increasingly large sample size. To do this, we used the 11 female-phase ranges (of daughters and mothers, each with their own phases) for which we had over 1500 focal location points (Table 2.S2). For each of these female-phases, we calculated a range using only the first 100 points, then using only the first 200 points, then the first 300 points, and so on, up to 2000 points (or the largest multiple of 100 points for that range). These ranges were calculated using the same method as described in the main text; most importantly, the h (smoothing) value was chosen by running multiple iterations of the kernel density utilization distribution with progressively smaller and smaller h-values, and then calculating the 95% isopleth polygons for each utilization distribution. The h-value chosen was the smallest (i.e. least smoothing) that still maintained a single polygon at the 95% isopleth (see main text for more details).

Thus, for all 11 female-phase ranges, we calculated the size of the range using only the first 100 points, the first 200 points, etc, up to 2000 points. We then calculated a linear mixed model (using the lme function from the nlme package, Pinheiro et al. 2018) with range size (in hectares) as the response variable, number of location points

included as the only fixed effect, and a unique identifier for each female-range combination as a random effect. The number of location points was coded as a factor and helmert contrasts were set, such that each set of ranges (ex. those calculated from 100 points) was compared to all subsequent sets (ex. those calculated from 200, 300, 400, etc points).

Figure 2.S3 shows the relationship between residual range size (after removing the variation associated with the female-range random effect) and the number of points included in the delineation of that range. There is a clear break between the 400 and 500 point ranges: ranges calculated using 100, 200, 300, and 400 points were significantly smaller than ranges calculated using more points (100-point ranges vs all 200+ point ranges: $b \pm SE$ = -8.74 ± 0.747, t = -11.71, $p < 0.0001$; 200-point ranges vs all 300+ point ranges: $b \pm SE$ = -5.67 ± 0.787, t = -7.20, $p < 0.0001$; 300-point ranges vs all 400+ point ranges: $b \pm SE$ = -5.28 ± 0.833, t = -6.34, $p < 0.0001$; 400-point ranges vs all 500+ point ranges: $b \pm SE$ = -4.30 ± 0.884, t = -4.87, $p < 0.0001$), whereas ranges calculated with 500 points were not significantly different from those calculated using more points (500-point ranges vs all 600+ point ranges: $b \pm SE$ = -1.46 ± 0.941, t = -1.55, $p = 0.123$). Thus, 500 points was determined to be the number of location points required for the calculation of a relatively stable range, and was therefore chosen as the minimum number of points required for a range to be included in the size and overlap analyses.

Supplementary Figures

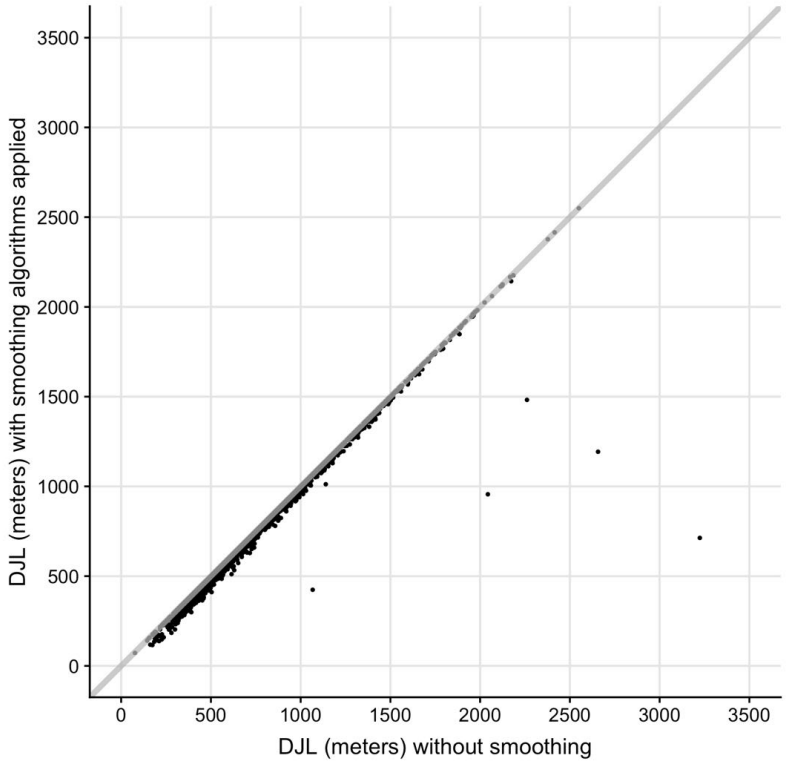

Figure 2.S1 The length of each focal follow's DJL using the unsmoothed (raw) location points (x-axis) plotted against the DJL using the smoothed (adjusted) location points (y-axis)

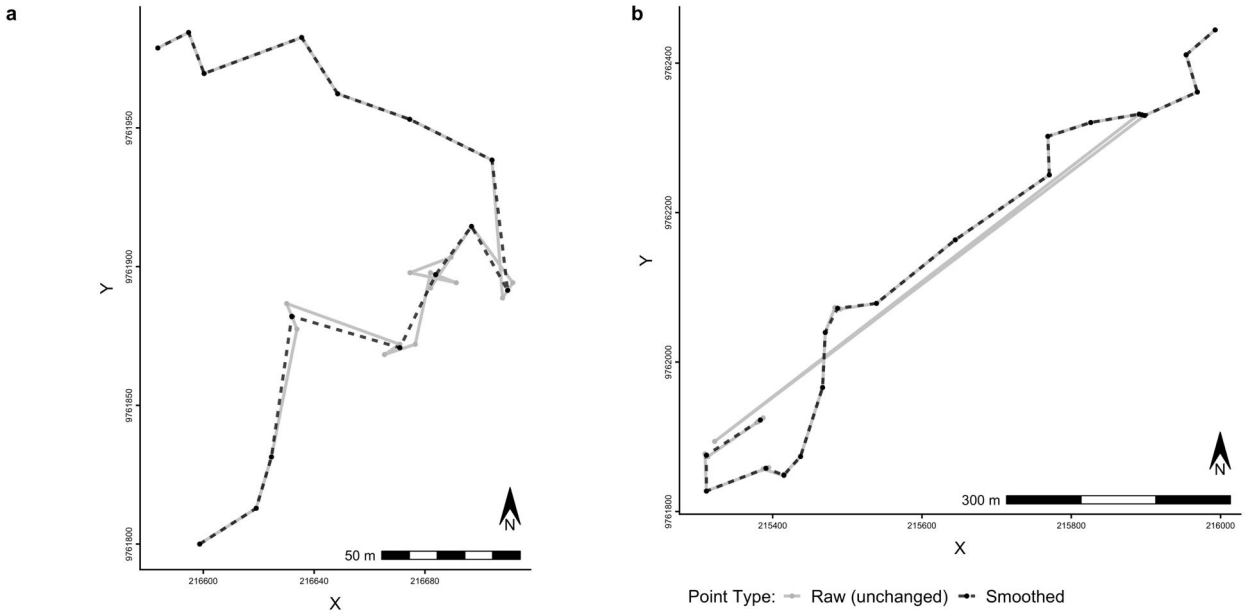

Figure 2.S2 Examples of follows with unsmoothed (raw) and smoothed (adjusted) points: the light grey line shows the track between the unsmoothed (raw) points and the black dashed line shows the track between the smoothed (adjusted) points; (a) has several smoothed imprecise stops, (b) has a smoothed impossible jump

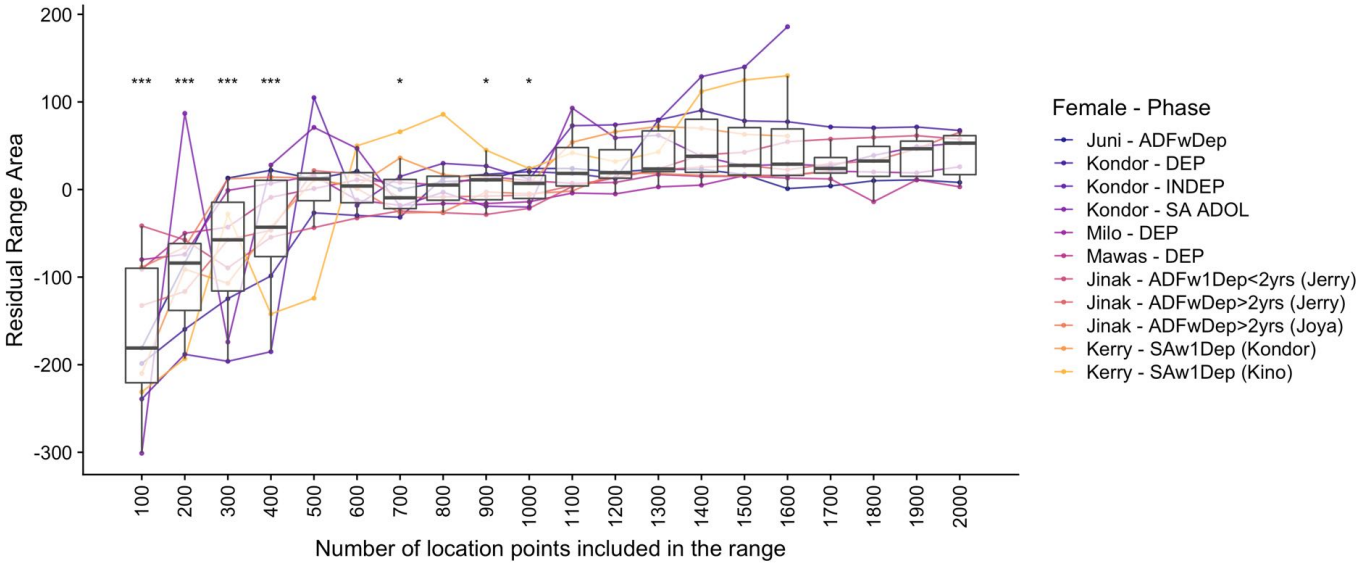

Figure 2.S3 The relationship between residual range size (after removing the variation associated with the female-range random effect) and the number of points included in the calculations of that range

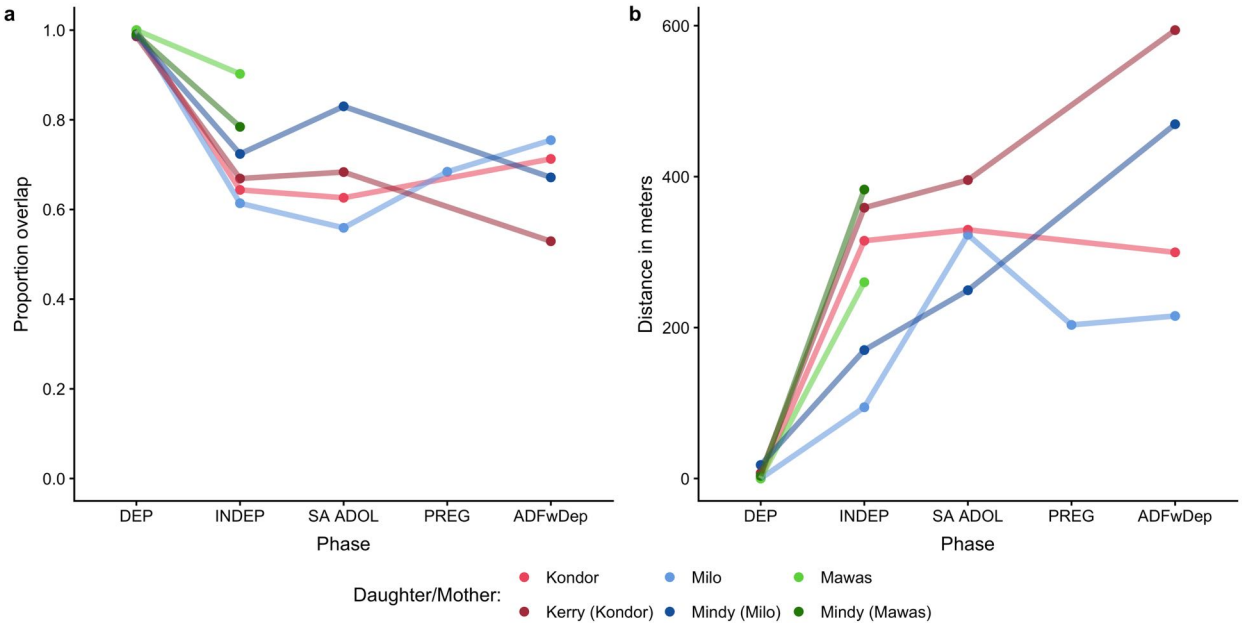

Figure 2.S4 (a) Daughters' and their mothers' (a) phase range overlap of, and (b) shift from, the daughters' natal range (i.e. her DEP phase range)

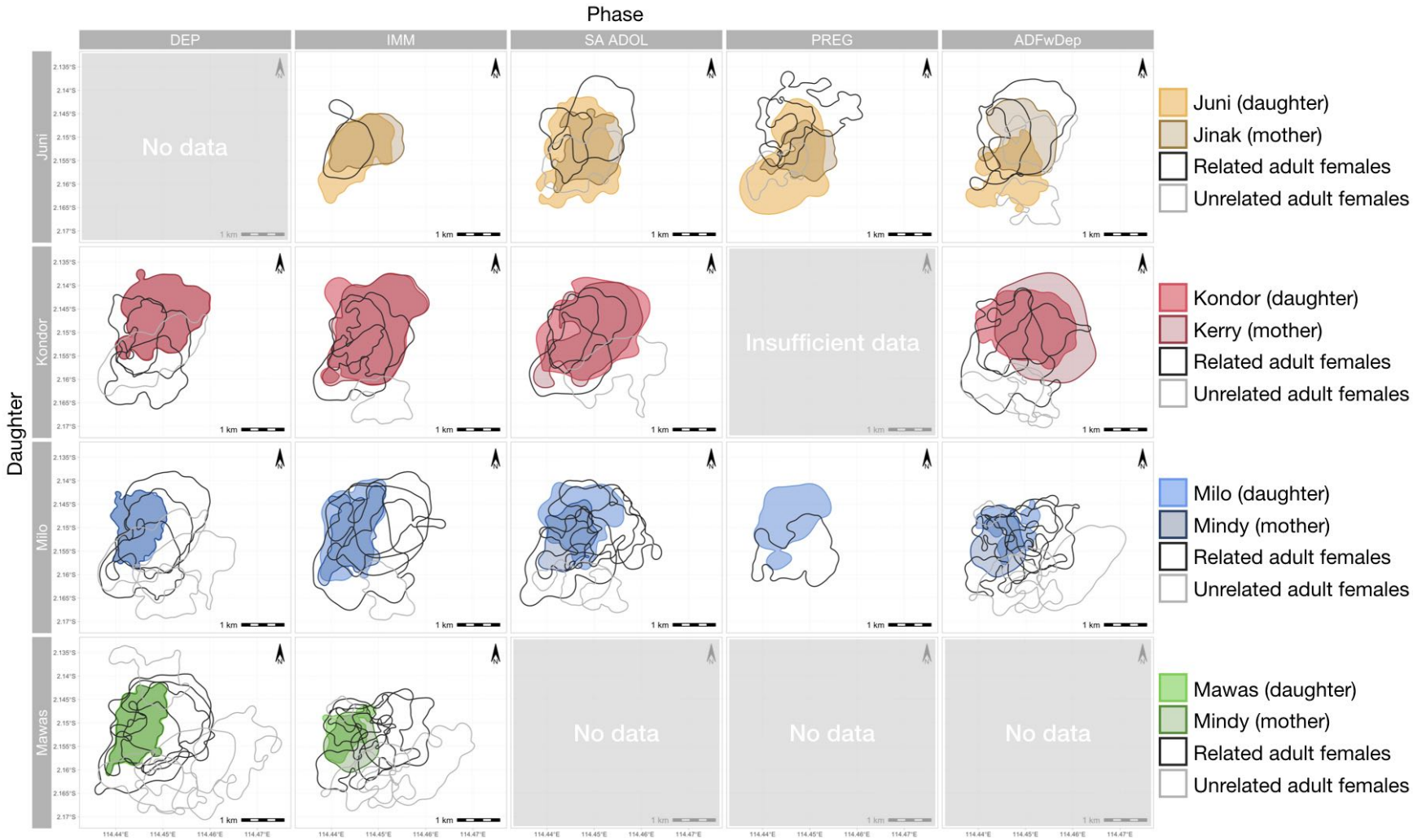

Figure 2.S5 Maps showing the phase ranges of each daughter, her mother, and all related and unrelated females included in the overlap analysis

Supplementary Tables

Table 2.S1 Dates, ages, durations, and sample sizes of the data sub-setted by *daughters' phases*; all sample sizes refer to focal follow hours of the corresponding female

Daughter	Date of Birth	Phase	Phase Start Date	Phase End date	Age at phase start (years)	Age at phase end (years)	Phase Duration (years)	Daughter sample size (hours)	Mother ID	Mother Sample size (hours)	Related ADFs[c] ID - Sample size (hours)	Unrelated ADFs[c] ID - Sample size (hours)
Juni	1994-01-01 (estimated)	INDEP	2003-07-07	2004-01-11	9.51	10.03	0.51	285	Jinak	370	Mindy - 254	(none)
		SA ADOL	2004-01-12	2005-06-09	10.03	11.44	1.41	319		1115	Mindy - 637 Kerry - 416	Sumi - 839
		PREG	2005-06-10	2006-02-09	11.44	12.11	0.67	357		407	Mindy - 479 Kerry - 277	Sumi - 346
		ADFwDep	2006-02-10	2008-02-09	12.11	14.11	2.00	1031		914	Mindy - 1000 Kerry - 745	Sumi - 321 Desy - 289
Kondor	1999-01-01 (estimated)	DEP[a]	2007-01-01	2007-03-12	8.00	8.19	0.19	62	Kerry	NA	NA	NA
		DEP	2003-07-07	2007-03-12	4.51	8.19	3.68	1274		1216	Jinak - 2501 Juni - 591 Mindy - 1816	Sumi - 1610
		INDEP	2007-03-13	2009-01-12	8.19	10.03	1.84	800		718	Jinak - 751 Juni - 802 Mindy - 1063	Desy - 361
		SA ADOL	2009-01-13	2011-06-14	10.03	12.45	2.41	1000		834	Jinak - 304 Juni - 736 Mindy - 752	Sidony - 387
		PREG	2011-06-15	2012-02-14	12.45	13.12	0.67	131[b]		119[b]	(none)	(none)
		ADFwDep	2012-02-15	2014-05-30	13.12	15.41	2.29	475		546	Jinak - 507 Juni - 607 Mindy - 629	Desy - 489 Inul - 283

Milo	2001-01-01 (estimated)	DEP[a]	2008-07-15	2011-09-05	7.53	10.67	3.14	901	Mindy	NA	NA	NA
		DEP	2003-07-07	2011-09-05	2.51	10.67	8.16	3852		3653	Jinak - 3596 Juni - 2201 Kerry - 2829	Desy - 654 Sidony - 458 Sumi - 1610
		INDEP	2011-09-06	2013-10-25	10.68	12.81	2.14	552		571	Jinak - 408 Juni - 557 Kerry - 404 Kondor - 301	Desy - 297
		SA ADOL	2013-10-26	2015-04-14	12.82	14.28	1.46	453		475	Jinak - 410 Juni - 452 Kerry - 514 Kondor - 445	Desy - 273 Inul - 444
		PREG	2015-04-15	2015-12-14	14.28	14.95	0.67	295		211[b]	Juni - 332	(none)
		ADFwDep	2015-12-15	2017-12-31	14.95	17.00	2.05	317		367	Jinak - 267 Juni - 310 Kerry - 406 Kondor - 465	Desy - 297 Inul - 378 Pinky - 492 Tina - 356
Mawas	2008-07-15	DEP[a]	2014-11-15	2016-02-24	6.34	7.61	1.28	172	Mindy	NA	NA	NA
		DEP	2008-07-15	2016-02-24	0.00	7.61	7.61	2360		2360	Jinak - 1503 Juni - 2398 Kerry - 2112 Kondor - 1012	Cinta - 297 Desy - 924 Inul - 750 Pinky - 358 Sidony - 764
		INDEP	2016-02-25	2017-12-31	7.61	9.46	1.85	358		367	Juni - 256 Kerry - 358 Kondor - 361 Milo - 258	Desy - 297 Inul - 322 Pinky - 380 Tina - 356

[a] Note that for daughters' day journey length and association with males analyses, only data after the mother's next offspring (i.e. the daughter's younger sibling) was born is included in the DEP phase.
[b] Sample size too small to calculate a range (therefore not included in range size and overlap analyses).
[c] Only adult females (ADFs) with large enough sample sizes to calculate a range (and which are therefore included in range size and overlap analyses) are listed.

Table 2.S2 The 'female - phase' ranges that included at least 1500 points, used to established a minimum number of points required to reach a relatively stable range size

Female	Mother or Daughter	Phase	Youngest Dependent Offspring	Total Point Count	Female - Phase Range ID
Juni	D	ADFwDep	NA	2113	Juni - ADFwDep
Kondor	D	DEP	NA	2549	Kondor - DEP
Kondor	D	INDEP	NA	1628	Kondor - INDEP
Kondor	D	SA ADOL	NA	2059	Kondor - SA ADOL
Milo	D	DEP	NA	7704	Milo - DEP
Mawas	D	DEP	NA	4715	Mawas - DEP
Jinak	M	ADFw1Dep<2yrs	Jerry	2849	Jinak - ADFw1Dep<2yrs
Jinak	M	ADFwDep>2yrs	Jerry	3158	Jinak - ADFwDep>2yrs
Jinak	M	ADFwDep>2yrs	Joya	1740	Jinak - ADFwDep>2yrs
Kerry	M	SAw1Dep	Kondor	1623	Kerry - SAw1Dep
Kerry	M	SAw1Dep	Kino	1692	Kerry - SAw1Dep
Mindy	M	ADFwDep>2yrs	Milo	4531	Excluded because high redundancy w/ Milo - DEP
Mindy	M	ADFw2Dep	Mawas	2203	Excluded because high redundancy w/ Mawas - DEP

Table 2.S3 Specific details about each model included in the analysis

Analysis	Outcome variable	Type of model	Fixed effects	Random effects (intercept)	Other details
Daughter's daily travel	DJL in meters (square root transformed to improve the normality of the model residuals)	LMM	Daughter's Phase[a] Fruit availability (of month of the follow) Proportion of day spent on the ground Proportion of day spent alone	Daughter's ID nested in mother's ID	
Mother's daily travel	DJL in meters (square root transformed to improve the normality of the model residuals)	LMM	Mother's Phase[a] Fruit availability (of month of the follow) Proportion of day spent on the ground Proportion of day spent alone	Mother's youngest offspring's ID nested in mother's ID	
Daughter's phase range size	Range area in hectares	LMM	Daughter's Phase[a] Mean fruit availability	Daughter's ID nested in mother's ID	
Mother's phase range size	Range area in hectares	LMM	Mother's Phase[a] Mean fruit availability	Mother's youngest offspring's ID nested in mother's ID	
Daughter-mother association time	Proportion of total phase time that daughters spent in association with their mothers	LMM	Daughter's Phase[a] Mean fruit availability	Daughter's ID nested in mother's ID	
Daughter – all adult female association time	Proportion of total phase time that daughters spent in association with each adult female	LMM	Daughter's Phase[a] Relationship (mother, related female, unrelated female)[b] Relationship × Phase Mean fruit availability	Adult females' ID nested in the daughter's ID	For each daughter, only females with whom the daughter had >0 phase range overlap and/or >0 proportion of time spent in association during at least one phase, were included
Daughter – all adult female association time, *post-hoc per-phase tests*	*For each phase:* Count of minutes that daughter spent in association with each adult female	GLMMs with Poisson distributions	Relationship (mother, related female, unrelated female)[b] Mean fruit availability Log of the total number of observation minutes (offset)	Daughter's ID	One model for each phase

Daughter – adult male association time	Proportion of total phase time that each daughter spent with each morph of adult male	LMM	Daughter's Phase[a] Male morph Male morph × Phase Mean fruit availability	Daughter's ID nested in her mother's ID	
Daughter-adult male association time, *post-hoc per-phase tests*	*For each phase:* Count of minutes that daughter spent in association with each morph of adult male	GLMMs with Poisson distributions	Male morph Mean fruit availability Log of the total number of observation minutes (offset)	Daughter's ID	
Daughter's association with males, effect on association with adult females	Proportion of each day that daughter spent in association with an adult female	LMM	Proportion of the day in association with an adult male Fruit availability (of month of the follow)	Daughter's phase nested in daughter's ID	Only INDEP, SA ADOL, and PREG phases included
Daughter's exploration in association with adult males	Whether or not each SA ADOL phase location point was inside the INDEP range	Binomial GLMM with a corCAR1 correlation structure (to account for temporal autocorrelation between points)	Male in association (yes/no)	Daughter's ID	Only the 3 daughters for whom whom we had INDEP and SA ADOL phases were included
Overlap with daughter's natal range	Singular directional overlap values; the proportion of individual's post-DEP phase range overlapped by the natal range (daughter's DEP range)	LMM	Daughter's Phase[a] Individual's class (mother or daughter)	Grouping variable for each mother-daughters dyad	Includes only the 3 mother-daughter dyads for whom we had a natal range (i.e. did not include Juni-Jinak)
Shift from daughter's natal range	Euclidian distance between the individual's post-dependence phase range centroid and the natal range (daughter's DEP range) centroid	LMM	Daughter's Phase[a] Individual's class (mother or daughter)	Grouping variable for each mother-daughters dyad	Includes only the 3 mother-daughter dyads for whom we had a natal range (i.e. did not include Juni-Jinak)
Daughter-mother phase range overlap	Dyadic overlap value between daughters' and mothers' ranges	GLMM with a beta distribution	Daughter's Phase[a] Mean fruit availability	Daughter's ID nested in mother's ID	
Daughter-mother phase range shifting	Euclidian distance between the centroids of daughters' and their mothers' ranges	LMM	Daughter's Phase[a] Mean fruit availability	Daughter's ID nested in mother's ID	

Daughter – all adult female phase range overlap	Dyadic overlap value between daughters' and each adult females' ranges	LMM	Daughter's Phase[a] Relationship (mother, related female, unrelated female)[b] Relationship × Phase Mean fruit availability	Adult female's ID nested in the daughter's ID	For each daughter, only females with whom the daughter had >0 proportion overlap during at least one phase were included
Daughter – all adult female phase range overlap, *post-hoc per-phase tests*	*For each phase:* Dyadic overlap value between daughters' and each adult females' ranges	LMM	Relationship (mother, related female, unrelated female)[b] Mean fruit availability	Daughter's ID	One model for each phase except PREG, for which the sample size was too small

[a]Phase was always set to a polynomial contrast
[b]Relationship was always set to a planned contrast of 1) mothers compared to unrelated adult females, and 2) mothers compared to other related adult females

Table 2.S4 The post-hoc per-phase model parameters (fixed effects) of the proportion of time that daughters spent in association with their mothers compared to with each other related and unrelated adult female, as well as the mean phase fruit availability (poisson GLMMs)

Effect		Related ADF vs Mothers					Unrelated ADF vs Mothers					Mean fruit availability					
Parameter		b	SE	Z	p		b	SE	Z	p		b	SE	Z	p		n
Phase	DEP	-4.113	0.006	-668.800	< 0.0001	***	-11.182	0.196	-57.000	< 0.0001	***	-0.026	0.022	-1.200	0.244		20
	INDEP	-4.174	0.019	-218.870	< 0.0001	***	-7.627	0.087	-87.520	< 0.0001	***	0.571	0.272	2.100	0.036	*	20
	SA ADOL	-3.389	0.023	-144.620	< 0.0001	***	-5.021	0.041	-122.700	< 0.0001	***	-0.044	0.483	-0.090	0.928		16
	PREG	-2.536	0.154	-16.454	< 0.0001	***	-1.585	0.107	-14.803	< 0.0001	***	0.600	0.530	1.133	0.257		5
	ADFwDep	-0.666	0.028	-23.750	< 0.0001	***	-4.211	0.133	-31.582	< 0.0001	***	0.861	0.513	1.678	0.093	·	18

Table 2.S5 The post-hoc per-phase model parameters (fixed effects) of the time that daughters spent in association with unflanged males compared to flanged males, as well as the mean phase fruit availability (poisson GLMMs)

Effect		Unflanged vs Flanged					Mean fruit availability					
Parameter		b	SE	Z	p		b	SE	Z	p		n
Phase	DEP	1.581	0.063	25.180	< 0.0001	***	-5.608	3.398	-1.650	0.099	·	6
	INDEP	2.191	0.043	51.450	< 0.0001	***	0.370	0.106	3.480	< 0.0001	***	8
	SA ADOL	2.159	0.015	148.150	< 0.0001	***	-0.044	0.049	-0.900	0.370	***	6
	PREG	-0.032	0.038	-0.848	0.396		-0.380	0.100	-3.778	< 0.0001		6
	ADFwDep	0.520	0.051	10.218	< 0.0001	***	0.130	0.193	0.674	0.500		6

Table 2.S6 The post-hoc per-phase model parameters (fixed effects) of the dyadic overlap value for daughters and their mothers compared to daughters and each other related and unrelated adult female, as well as the mean phase fruit availability (LMMs)

Effect		Related ADF vs Mothers					Unrelated ADF vs Mothers					Mean fruit availability				
Parameter		b	SE	t	p		b	SE	t	p		b	SE	t	p	n
Phase	DEP	-0.704	0.059	-11.897	< 0.0001	***	-0.923	0.063	-14.761	< 0.0001	***	-0.022	0.044	-0.507	0.701	20
	INDEP	-0.412	0.068	-6.033	< 0.0001	***	-0.610	0.085	-7.212	< 0.0001	***	0.048	0.034	1.419	0.292	20
	SA ADOL	-0.189	0.094	-2.004	0.070	·	-0.354	0.108	-3.282	0.007	**	0.016	0.047	0.348	0.787	16
	PREG	NA	NA	NA	NA		NA	NA	NA	NA		NA	NA	NA	NA	5
	ADFwDep	-0.088	0.064	-1.370	0.194		-0.225	0.069	-3.278	0.006	**	0.041	0.019	2.181	0.274	18

Chapter 3: Geographic contrast in responses to fruit scarcity by female Bornean orangutans (*Pongo pygmaeus spp*.)

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ABSTRACT

Animals living in seasonal, unpredictable, or harsh habitats employ ecological strategies in order to cope with scarcity in preferred resources; these can often be broadly categorized as dietary or ranging responses. Because of the geographic variation in their habitats and their behavioral flexibility, orangutans (genus *Pongo*) are an ideal taxon in which to investigate variation in ecological strategies used to cope with scarcity, and to test criteria that lead to area-switching rather than diet-switching. We present a natural experiment wherein we compare the influence of extreme fruit scarcity on the ranging patterns of female Bornean orangutans in two populations living under two different long-term ecological conditions: Wehea in Eastern Borneo, and Tuanan in Central Borneo. Wehea is a Dipterocarp forest habitat subject to long periods of extreme fruit scarcity with occasional supra-annual masts, while Tuanan is a peat-swamp forest habitat with relatively stable, predictable seasonal fluctuations in fruit availability and widespread high-quality fallback foods. Our results from an intra-population comparison at Tuanan show that, during a rare period of prolonged low fruit availability, female orangutans in this habitat significantly reduce the areas of their home ranges and likely incorporate ubiquitous fallback foods into their diets, thus employing a dietary response to scarcity. In contrast, female orangutans living in the fruit-scarce Wehea habitat are employing a ranging response to scarcity, ranging over vast areas in search of fruit and/or higher quality fallback foods. This inter-population comparison sheds light on the costs and benefits of dietary and ranging responses as ecological strategies for coping with scarcity.

KEYWORDS: Northeast Bornean orangutan, resource scarcity, home range size, area-switching, diet-switching

INTRODUCTION

Animals living in seasonal, unpredictable, or harsh habitats employ various ecological strategies in order to survive when their preferred resources are scarce (van Schaik et al. 1993). Across non-hibernating taxa, the numerous behavioral strategies for coping during periods of scarcity can be broadly categorized as dietary or ranging responses.

Dietary responses to scarcity occur when animals feed on alternative, less preferred resources, often termed "fallback foods," which may be of lower nutritional quality than preferred resources (Hemingway and Bynum 2005, Marshall et al. 2009). Fallback foods are often present in habitats at higher densities so energetic consequences of a lower quality diet can be offset by the reduced need to expend energy traveling to find food (van Schaik and Brockman 2005). Evidence of a reliance on fallback foods in response to seasonal fluctuations in resource availability has been observed across animal taxa, including among fish (e.g. sandpaper skates, Rinewalt et al. 2007), amphibians (e.g. frogs, Berazategui et al. 2007), marine mammals (e.g. fur seals, Fea et al. 1999), and terrestrial mammals (e.g. honey badgers, Begg et al. 2003; wild rabbits, Martins et al. 2002; and primates, Hemingway and Bynum 2005). Dietary responses can vary from slight shifts – i.e. incorporating small amounts of lower-quality foods as preferred foods become increasingly scarce – to more extreme switches: near-complete diet-switching from no-longer-available preferred foods to alternative food resources.

Ranging responses to scarcity involve spatio-temporal adjustments in animals' movement and travel patterns. Ranging responses can include relatively minor adjustments, for example increasing daily travel distance in order to harvest more widely-dispersed food sources (e.g. Francois' langur, Zhou et al. 2006), much larger changes such as range expansions, or even movement into different, phenologically asynchronous, areas or habitats in order to gain access to available resources – referred to as 'area-switching' (van Schaik and Brockman 2005). Area-switching occurs along many gradients and at different spatial scales, including movements up and down topographic gradients ("altitudinal migrations", e.g. giant pandas and golden takins, Wang et al. 2010; tortoises, Blake et al. 2012; greater sage-grouse, Pratt et al. 2017; see also cross-taxa review, Hsiung et al. 2018), movement between habitat types in a mosaic area (e.g. masked palm civets, Zhou et al. 2008; black-headed gulls, Schwemmer and Garthe 2008), and long-distance migration between distinct seasonal ranges (e.g. arctic terns, Egevang et al. 2010; moose, Ball et al. 2001; wildebeests, Holdo et al. 2009).

In general, when confronted with scarcity, an animal can prioritize a dietary response - which usually includes a reduction in movement and travel, or a ranging response - which usually involves an increase in movement and travel. It is unclear why and when primates prioritize one of these general strategies over another. However, it is important to note that dietary responses and ranging responses to scarcity are not mutually exclusive, and one is often a side-effect of the other. Diet-switching to lower quality, more widely available fallback foods may require and/or enable reduced daily travel and even a smaller home range size (e.g. Japanese macaques, Hanya et al. 2006; snub-nosed monkeys, Li et al. 2000). On the other hand, ranging responses such as habitat shifts may also include a change in diet, as the food resources available in the new habitat may differ from those in the previous/usual habitat (e.g. common brown lemurs, Sato 2013).

With respect to ranging responses, area-switching – the most "extreme" ranging response – is predicted to occur where an animal is following an energy-maximizing strategy and the potential costs associated with moving to, and ranging within, a new area are outweighed by the potential benefits of accessing the resources available in the new area (Hemingway and Bynum 2005). Specifically, we predict that animals will employ some degree of area-switching when 3 criteria are fulfilled: 1) the scarcity episode in the animal's current area is long in duration and strong in its severity, such that fallback foods are either not available or not sufficient; 2) other habitat with preferred foods (or higher quality fallback foods) – i.e. which is phenologically asynchronous and/or a different habitat type from the current area – must be accessible to the animal; and 3) the risks associated with ranging in the new area (in terms of within and between-species feeding competition, predation, etc.) must be low. In other words, the costs of staying (1) must be high enough that they outweigh the potential costs of travelling to (2) and ranging within (3) a new area. Which of these factors actually *drives* the ranging response may vary, but all 3 must be true in order for a ranging response to be an adaptive strategy for coping with scarcity.

Because of the geographic variation in their habitats and their behavioral flexibility, orangutans (genus *Pongo*) are an ideal taxon in which to investigate variation in ecological strategies used to cope with scarcity, and to test the criteria which we hypothesize will lead to area-switching. Orangutans are primarily frugivorous, semi-solitary, great apes (Wich et al. 2009). Across their geographic range, orangutans exhibit morphological, physiological, and behavioral variation, much of which can be linked to variation in the abundance and predictability of fruit availability in their habitats (van Schaik et al. 2009). Fruit production is consistently higher in the west (Sumatra) than in the east (Borneo), and peat swamp forests have relatively stable fruit productions over time, whereas dryland forests, especially masting dipterocarp forests, show more pronounced fluctuations (Wich et al. 2011).

Orangutans employ several ecological strategies for dealing with the high temporal variability in resource abundance within and across years in their habitats. When fruit is scarce, orangutans alter their activity budgets and spend less time in association with conspecifics, and more time resting, than when fruit is abundant. Furthermore, studies have shown extensive evidence of orangutans employing diet-switching to cope with scarcity (van Schaik et al. 2009) increasing their intake of non-fruit resources, including flowers, leaves, inner bark, and pith, when fruit is scarce (Morrogh-Bernard et al. 2009; Vogel et al. 2009; Bastian et al. 2010; Campbell-Smith et al. 2011).

Orangutans also alter their movement patterns in coordination with the spatio-temporal distribution of fruit. Evidence of changes in daily travel distance in correlation with fruit availability is mixed and likely driven by variations in association time with conspecifics (Singleton et al. 2009; Vogel et al. 2009; Harrison et al. 2010). However, there is a clear relationship between the degree of habitat heterogeneity and the size of female orangutan home ranges: in mosaic habitats, females have larger home ranges, and can therefore move between different habitat types to access asynchronously available resources (Singleton and van Schaik 2001; Singleton et al. 2009). Additionally, at some sites, local orangutan population densities correlate with local fluctuations in fruit availability (Danum Valley: Kanamori et al. 2016; Ketambe: Te Boekhorst et al. 1990; see also Spillman et al. 2017), and evidence of altitudinal migrations has been observed at at least one site (Ketambe: Buij et al.

2002). The spatial scale of these movements and migrations, suggests that individuals may be engaging in small-scale area-switching by exploiting different parts of their home ranges at different times.

Here, we present a natural experiment wherein we investigate the responses to scarcity in two populations of orangutans living under different ecological conditions: Wehea in Eastern Borneo, and Tuanan in Central Borneo. Wehea is a Dipterocarp forest habitat subject to long periods of extreme fruit scarcity with occasional supra-annual masts. Preliminary observations in a 1200-ha study area of Wehea Protected Forest suggested seasonal absences of local females (Ashbury et al. 2017). The Wehea habitat and orangutan population fulfill the 3 criteria under which we would expect some degree of area-switching to occur: 1) in between masting events, fruit scarcity is severe for up to several years in a row (SNS and R. Delgado, unpublished data); 2) the extremely varied topography of this forest and the overall altitudinal gradient (higher to the west) of the area may include variable and phenologically asynchronous resource availability across this landscape; additionally, orangutans in this population are known to have a high rate of ground-use (Loken et al. 2013; Loken et al. 2015; Ashbury et al. 2015), thus reducing the energetic cost of long-distance travel; and 3) the population density is very low and associations between orangutans are rare, suggesting that there is space for individuals to relocate temporarily without incurring social aggression or high intra-specific feeding competition costs (Spehar et al. 2016, Ashbury et al. 2017).

We compare the ranging patterns of female orangutans at Wehea with that of female orangutans at Tuanan, a peat-swamp forest with relatively stable, predictable seasonal fluctuations in fruit availability, widespread high-quality fallback foods, and the highest population density recorded among any wild Bornean orangutan population (van Schaik et al. 2005). In the well-studied Tuanan population, female orangutans live in relatively small (200-450 hectare) and very stable home ranges (Wartmann et al. 2010; van Noordwijk et al. 2012). Furthermore, we contrast the ranging patterns of females at Tuanan under 'normal' fruiting conditions, with those observed at the same site during a recent period of uncharacteristically prolonged fruit scarcity; after the widespread and severe forest fires across Borneo blanketed the Tuanan area in haze in 2015 (see Miettinen et al. (2017), Meijaard (2018) and Erb et al. (2018) for details), there was a period of approximately 2 years during which Tuanan experienced consistently low fruit availability.

Our natural experiment compares the influence of fruit scarcity on the space-use patterns of female Bornean orangutans living under two different long-term ecological conditions. First, we conducted an *intra*-population comparison at Tuanan, in which we compared female home range sizes before the 2015 fires, when habitat fruit levels were following predictable seasonal fluctuations, versus during the scarcity episode triggered by the fires. In this first comparison, we expected to see evidence of diet-switching, rather than area-switching, in response to scarcity. Second, we conducted an *inter*-population comparison between Tuanan and Wehea, in which we compare evidence of female ranging areas between Wehea, the fruit-scarce condition, and Tuanan, the fruit-stable condition. In this second comparison, we expect to see evidence of area-switching in response to the fruit scarce habitat at Wehea.

METHODS

Study Sites

Our comparative study uses data from two different wild orangutan populations: Central Bornean orangutans (*Pongo pygmaeus wurmbii*) in the Tuanan Mawas Reserve, Central Kalimantan, and Northeast Bornean orangutans (*Pongo pygmaeus morio*) in and around Wehea Protected Forest (WPF), East Kalimantan, both in Indonesia. Figure 3.1 shows the locations of these two sites, as well as more detailed maps of the study areas.

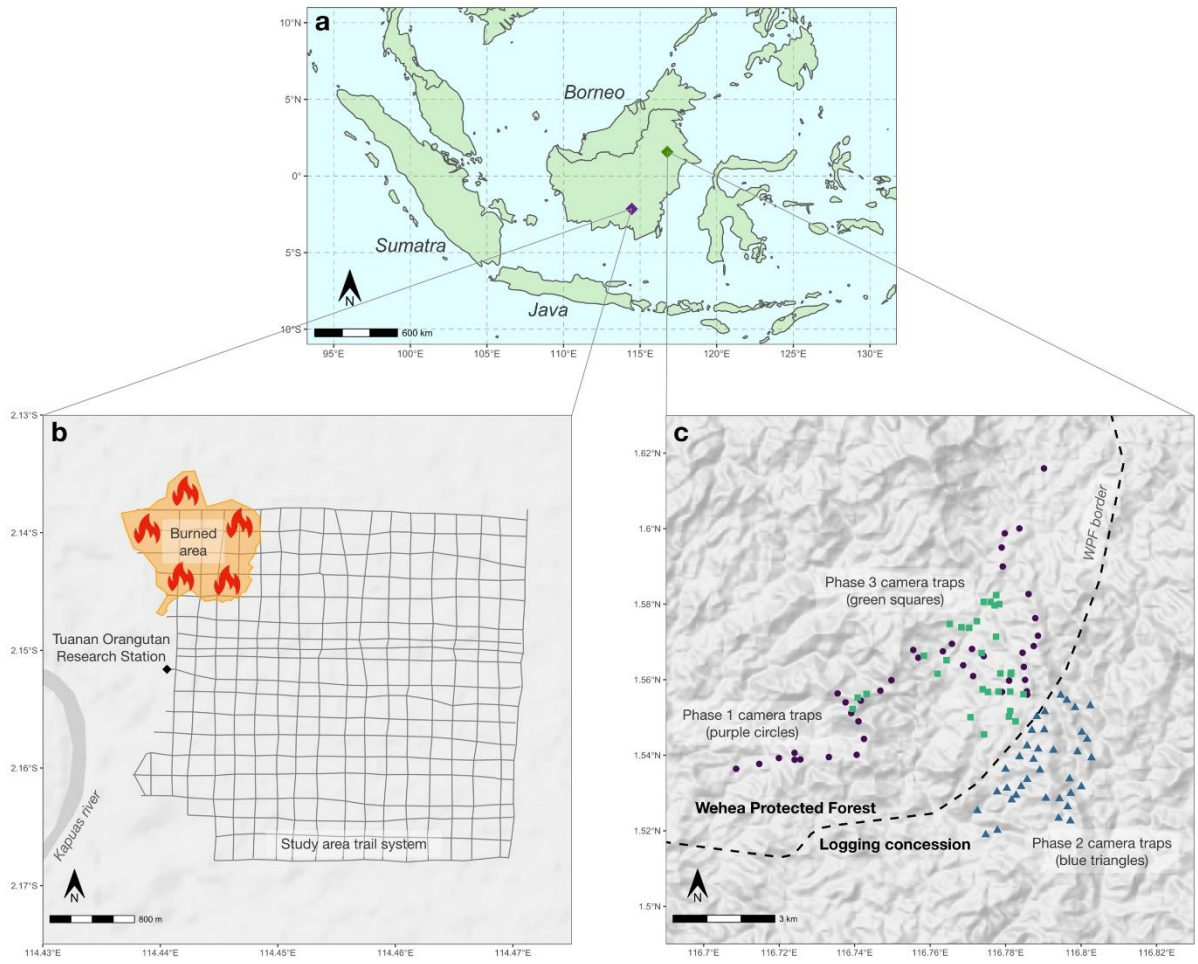

Figure 3.1: The locations of both field sites in Borneo (a), and larger scale depictions of the Tuanan study area, trail system, and area burned in 2015 (b), and the Wehea area and camera trap locations, coloured by phase (c). Both site maps are overlaid on Google topography maps.

Data collection at the Tuanan Orangutan Research Station (2.151° S; 114.374° E) in the Mawas Reserve, Central Kalimantan, Indonesia, took place between 2003 and 2017. The Tuanan study area is composed of homogeneous, formerly selectively-logged, peat-swamp forest. Under normal conditions, this forest experiences within-year seasonal fluctuations in fruit availability that are relatively predictable, with only short periods of low fruit availability (see Vogel et al. 2016 for details) (Fig. 3.2a). The 2015 forest fires in Borneo blanketed the Tuanan area in smoke and haze from August to October 2015, and burned a *ca.* 100-ha portion of the study area in October 2015. Subsequently, starting in November 2015, the Tuanan forest experienced an uncharacteristic drop in fruit availability, which remained uncharacteristically low for the next several months. The Tuanan area

is inhabited by Central Bornean orangutans (*P. p. wurmbii*) with a population density of 4.25 to 4.5 individuals/km^2 (van Schaik et al. 2005).

Data collection in and around Wehea Protected Forest (1.567° N; 116.771° E), East Kalimantan, Indonesia, took place between 2012 and 2017. Wehea Protected Forest (WPF) is a 38,000-hectare community-protected forest, consisting of lowland Dipterocarp, sub-montane, and montane forest types (for more details, see Spehar et al. 2015). Our study took place in the south-eastern part of WPF, which consists predominantly of relatively undisturbed lowland Dipterocarp forest. Some light selective logging took place in this area, but ceased in 1996. We also placed camera traps in an active logging concession which borders WPF to the east. This area consisted of lowland Dipterocarp forest subject to ongoing selective logging (for details, see Loken et al. 2015). The Wehea region experiences extreme long-term fruit scarcity (SNS and R. Delgado, unpublished data), with marked supra-annual mast fruiting events caused by ENSO cycles (Fig. 3.2c). The Wehea area is inhabited by Northeast Bornean orangutans (*P. p. morio*) with a population density of approximately 1 to 2 individuals/km^2 (Spehar et al. 2016, Ashbury et al. 2017).

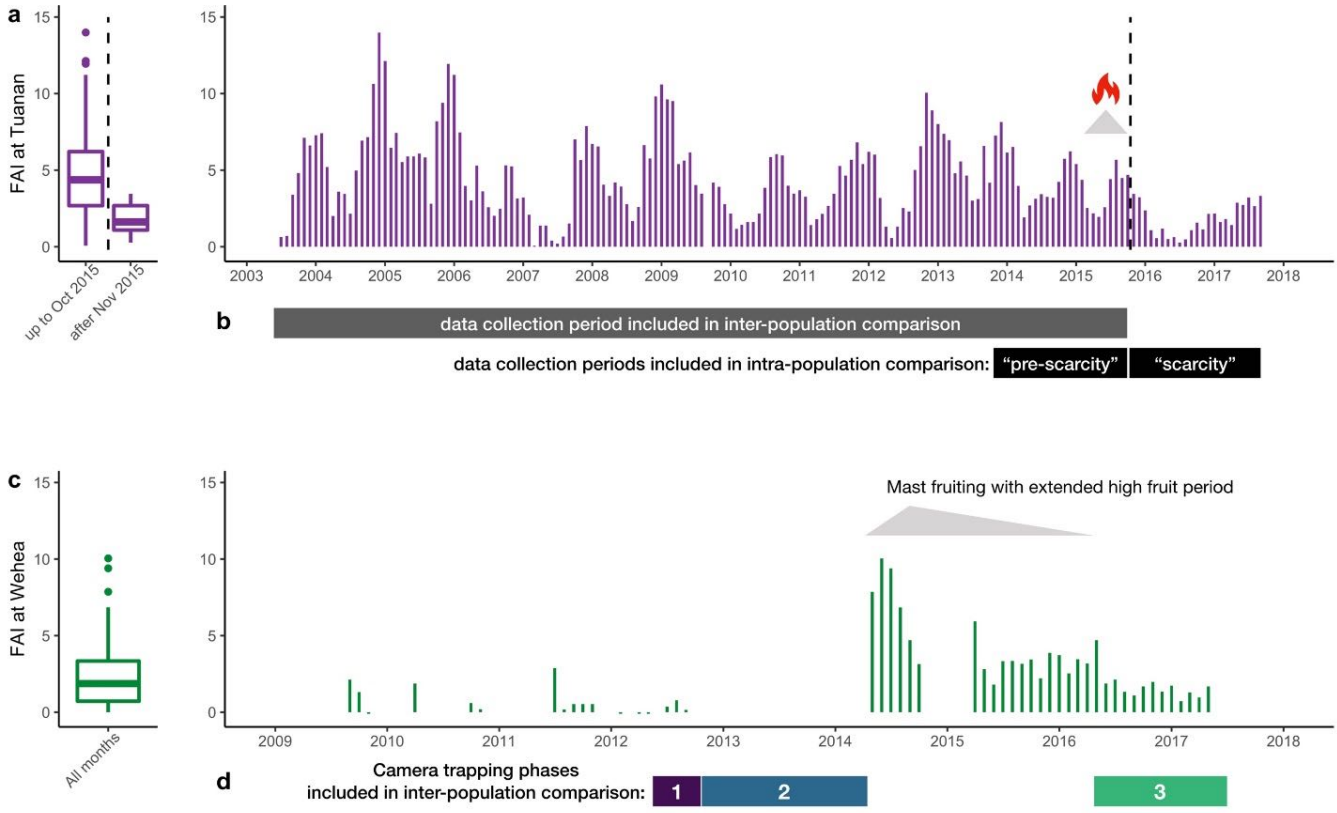

Figure 3.2: Timelines showing the fruit availability index (FAI) and data collection periods at each site, Tuanan (a, b) and Wehea (c, d). Blank spaces in the FAI timelines represent months wherein FAI data were not collected, while FAI values of 0 (occurred only at Wehea) are represented by short bars that hang below 0. Boxplots to the left of each FAI timeline (a, c) are meant to give a general idea of the overall FAI levels at each site. Important events are marked on the FAI timelines: the forest fires across Borneo (including in the Tuanan study area) in 2015 (a), and a mast fruiting at Wehea in 2014 (c). Below the FAI timelines, bars represent the duration and timing of data collection included in the analyses at each site: at Tuanan (b) the dark grey bar represents the data collection period included in the inter-population comparison, while the two shorter black bars indicate the 'pre-scarcity' and 'scarcity' periods included in the intra-population comparison, and at Wehea (d) the coloured bars represent the 3 phases of camera trapping included in the inter-population comparison.

Data collection

Habitat fruit availability data (presented in Figure 3.2) were collected at both study sites using standardized methods: marked trees in delineated plots were checked for fruit each month (for details, see Vogel et al. 2016). The monthly fruit availability index (FAI) is the percentage of stems bearing fruit. These data are credited to: Wehea 2009 to 2013 - SNS and R. Delgado, unpublished data; Wehea 2014 to 2017 - AMA and SNS, unpublished data; Tuanan 2003 to 2017 - Tuanan Orangutan Research Project, MAvN and E. Vogel.

Orangutan location data were collected using different methods and over different time periods at each site; Figure 3.2 outlines the overall timeline of data collection at both sites.

We collected data at Tuanan by direct observation of individually-identified orangutans during focal follows (Altmann 1974). Orangutans were found opportunistically by trained observers, and followed from morning nest until night nest for up to 10 days in a row. We noted the locations of focal orangutans at every night nest, as well as at every half-hour interval throughout the day, either by drawing points on printed maps of the study area trail system (pre-2012), or by making waypoints on hand-held Garmin GPS units (2012-2017). We used Garmin MapSource (v6), Garmin BaseCamp (v4) and ESRI's ArgGIS (v9.3) software to digitize hand drawn maps and to import GPS unit data. Furthermore, the borders of the burned area were also mapped by JMdB using a hand-held GPS unit.

We collected data at Wehea by indirect observation of orangutans using camera traps, as the Wehea-area orangutan population has a very low density and individuals exhibit very elusive behavior. Data collection in the Wehea area took place in 3 phases:

1. Ground-level camera trapping in Wehea Protected Forest (WPF) from May to October 2012,
2. Ground-level camera trapping in an active logging concession adjacent to WPF from Oct 2012- April 2014,
3. Ground-level and canopy camera trapping in WPF from May 2016 to July 2017.

Summary data are included in Table 3.1. Table 3.S1 gives a more detailed overview of the camera trap station locations, dates, and active days. Further details about Phase 1 camera trap deployment can be found in Loken et al. (2013; 2015), and Spehar et al. (2015). Details about Phase 2 camera trap deployment can be found in Loken et al. (2013). Details about Phase 3 camera trap deployment are as follows:

Between May 2016 and July 2017, we placed six Reconyx Hyperfire HC500 camera traps and twenty-four Bushnell Aggressor HD Red-Glow camera traps in the study area of a concurrent direct observation study of orangutans in WPF (direct observation study directed by AMA and SNS, unpublished data). The study area was approximately 1200-ha, and was divided into 7 'zones' of approximately equal area (~170 ha). We installed a primary camera trap station along a prominent ridgeline in each zone and left it in place for the entire duration of Phase 3 (May 2016 to July 2017; totaling 5316 camera trap days). We also installed a second arboreal camera trap station in each zone, approximately 15 to 30 meters above the ground facing down along fruiting *Ficus* vines hanging from large dipterocarp trees, from May to October 2016 (1950 camera trap days). Additionally, we moved seven secondary camera trap stations between various locations (old and currently used roads, ridge

lines, and trees fallen across deep ravines) every 2-6 months from November 2016 to May 2017 (1819 camera trap days). All camera trap stations included two cameras which were set up to take 3 photos for every trigger with no delay (Reconyx) or a 1 second delay (Bushnell) between triggers.

Additionally, we installed 2 camera trap stations at small salt-licks in the study area from May 2016 to July 2017; the smaller salt-lick camera trap station consisted of 2 cameras (647 camera trap days), and the larger one had 2 to 4 cameras (1288 camera trap days). Photo and trigger settings for the salt-lick cameras varied: we set cameras to take either 1 or 3 photos, with a delay of 1 second up to 5 minutes. We chose these settings based on the availability of the field team. Because the salt-licks were frequented by many animals, cameras here would run out of battery and/or memory relatively quickly, and so we set the cameras to take 3 photos per trigger with faster trigger reset times when a field team was present to service the cameras regularly, otherwise they were set to take 1 photo per trigger, with a 5- or 10-minute reset time. Figure 3.S1 shows some examples of Phase 3 camera trap stations, and Figure 3.S2 shows a map of the study area, the zones and the locations of the camera trap stations.

Table 3.1 Basic overview data of the 3 phases of camera trap deployment at Wehea

Phase	General location	No. of station locations	No. of active camera trap days	Original study
1	Wehea Protected Forest	43	8'080	Loken et al. (2013, 2015); Spehar et al. (2015)
2	Logging concession	36	15'775	Loken et al. (2013)
3	Wehea Protected Forest	30	11'020	This study

Wehea data preparation for inter-population comparison

We manually extracted all photos of orangutans from the total set of camera trap photos. We then grouped all orangutan photos into 'records': one record consisted of a set of photos of one individual orangutan (or one mother-offspring unit) taken at a single camera trapping station, with less than a 1-hour gap between photos. We assigned identities to all female orangutans in as unbiased a way as possible: two observers (AMA and SNS) independently assessed the photos of the female orangutans without any knowledge of when and where each photo record was captured, and grouped records into individual IDs.

We created two datasets based on the agreement or lack thereof between the two observers: a 'split' and a 'lumped' dataset. The 'split' scenario represents the most conservative estimate of female IDs – where at least one observer assigned multiple IDs to a group of records, the records were split into separate IDs. The 'lumped' scenario represents the less conservative but equally plausible estimate of female IDs – where at least one observer assigned a single ID to a group of records, the records were lumped into that single ID. Each record was assigned the location of the camera trap station that captured it and these locations were used in the subsequent spatial analyses. We conducted two separate analyses: a 'split' scenario analysis representing the most conservative estimate of female space-use, and a 'lumped' scenario analysis representing an equally plausible and more extreme estimate of female space-use at Wehea.

See Supplementary Methods 1 for more details about the process by which IDs were assigned to camera trap records and the two datasets were created.

Tuanan data preparation for inter-population comparison

For the inter-population comparison, we included only data collected at Tuanan before October 2015 (i.e. before the prolonged period of scarcity began), as this represents the relatively undisturbed condition of this orangutan population. We also focused on the five adult females who have been followed the most extensively since the beginning of the Tuanan study in 2003. For each of these females, we have at least 1900 follow hours (range = 1987 to 10872) and at least 2200 location points each (range = 2201 to 12000). As such, we are certain of the boundaries of their home ranges, and we are confident that they do not move into areas into which we have not followed them. For those females who first reproduced between 2003 and 2015 (n = 2), only location data from after their first offspring was born were included, in order to keep the comparison with Wehea consistent between parous females only.

In order to obtain estimates of these females' space-use that were comparable between Wehea and Tuanan, despite the difference in data collection methods, we used iterations and sub-setting of the Tuanan location data (collected during focal follows) in such a way as to mimic the Wehea data (collected from camera traps). This process is explained in detail in Supplementary Methods 2. Its output was 10,000 iterations of a 'split' and of a 'lumped' scenario for these five females at Tuanan – wherein the number of location points per female in each scenario in each iteration matched the number of location points obtained in the 'split' and 'lumped' datasets of Wehea (see Results).

Data analysis for Tuanan intra-population comparison

For the intra-population comparison of female space-use, we used a subset of Tuanan data from November 2013 to September 2017, which was divided into "pre-scarcity" (24 months preceding November 2015) – during which fluctuations in habitat fruiting conditions were within the long-term normal range, and "scarcity" (starting in November 2015 and including the subsequent 23 months) – during which habitat fruiting conditions were consistently and uncharacteristically low (see Figure 3.2a & b). We included all parous females for whom we had at least 300 location points in each condition (n = 9), as these were the females for whom we had location data temporally well-distributed across the time intervals of both conditions ("pre-scarcity" and "scarcity"). We thus excluded 15 females who were observed ranging in the Tuanan study area during this time but for whom we did not have sufficient data to calculate reliable home ranges during both conditions.

Previous studies have shown that the minimum convex polygon (MCP) method of home range delineation is significantly influenced by sample size – with increasing sample size leading to larger home ranges (Wartmann et al. 2010). We therefore used iterations to calculate home ranges: we calculated the 95% MCP area of 100 randomly selected points per female, from each condition (pre-scarcity and scarcity), 1000 times. In this way, we could keep the sample sizes across individuals consistent (100 points per individual per iteration) without having to discard locations of any individuals, which could lead to underestimations of home range sizes. This gave us one thousand home range areas (one per iteration) for each female in each of the conditions. We also calculated the overlap area between each home range (each iteration in each condition for each female) and the

burned portion of the study area. Figure 3.S5 shows an example of one pre-scarcity and one scarcity iteration of females' 95% MCP home ranges.

To compare pre-scarcity and scarcity home range areas, we constructed a linear mixed model with 95% MCP area as the outcome variable and condition (pre-scarcity or scarcity) as the only fixed effect. Random effects were condition (pre-scarcity or scarcity) as a random slope and female ID as a random intercept. To account for heterogeneity of variance between the two conditions, we included a constant variance structure (varIdent) in the model. The model was fit by maximum likelihood.

Data analysis for inter-population comparison

In order to compare female space-use between the two populations, we analyzed the spread of locations at which each female was recorded, in two separate analyses: one for the 'split' scenario and one for the 'lumped' scenario. In each analysis, for each female at Wehea, and for each of the 5 included Tuanan females for each of the 10,000 iterations, we calculated the maximum inter-location distances of the (simulated, in the case of Tuanan) camera trap locations at which they were recorded. Females at Wehea who were only photographed at a single location and, within each Tuanan iteration, females who were only recorded at a single simulated camera trap location, were removed from the datasets. In other words, all maximum inter-location distance values of 0 meters were removed from the datasets and excluded from the statistical analyses.

We statistically compared female space-use at Wehea to that at Tuanan in 2 ways. First, the maximum inter-location distance values across iterations for each female at Tuanan were averaged, and these five values (one per female) were compared to the values of the females at Wehea using Mann-Whitney U tests. Second, we calculated the 95% quantile of all Tuanan maximum inter-location distance values from all iterations, and checked whether or not the Wehea females' maximum inter-location distances fell above or below this value.

Software

We conducted all spatial and statistical analyses in R version 3.5.1 (R Core Team 2018). We calculated MCP ranges and the overlap between these ranges and the burned area using the adehabitatHR package (Calenge 2006), and for all other spatial calculations (including the inter-location distances) we used the sf package (Pebesma 2018). We used the nlme package for linear mixed modelling (Pinheiro et al. 2018). Maps were created using the ggmap (Kahle and Wickham 2013) or rnaturalearth (South 2017) packages, as well as the ggspatial (Dunnington 2018), and ggplot2 (Wickham 2016) packages.

RESULTS

Tuanan pre-scarcity vs scarcity intra-population comparison

The mean home range area of adult females at Tuanan during a period of normal fruit availability (pre-scarcity) was 170 hectares (range = 46 to 404 ha, n_{ranges} = 9000, $n_{individuals}$ = 9), and during the scarcity episode this dropped to 119 hectares (range = 42 to 265 ha, n_{ranges} = 9000, $n_{individuals}$ = 9). The home range areas were significantly smaller during the period of fruit scarcity, than they were pre-scarcity (LMM: n_{ranges} = 18000, $n_{individuals}$ = 9, $b \pm SE$ =-50.23 ± 15.63, t = -3.21, $p < 0.005$). Figure 3.3 shows the difference between the iterated 95% MCP ranges for each condition per female. While the degree of decrease from the pre-scarcity to scarcity condition varies between individuals, all adult females except for one (Desy) show a decrease in home range size, and individuals with the largest home ranges pre-scarcity generally show the largest degree of decrease in home range size.

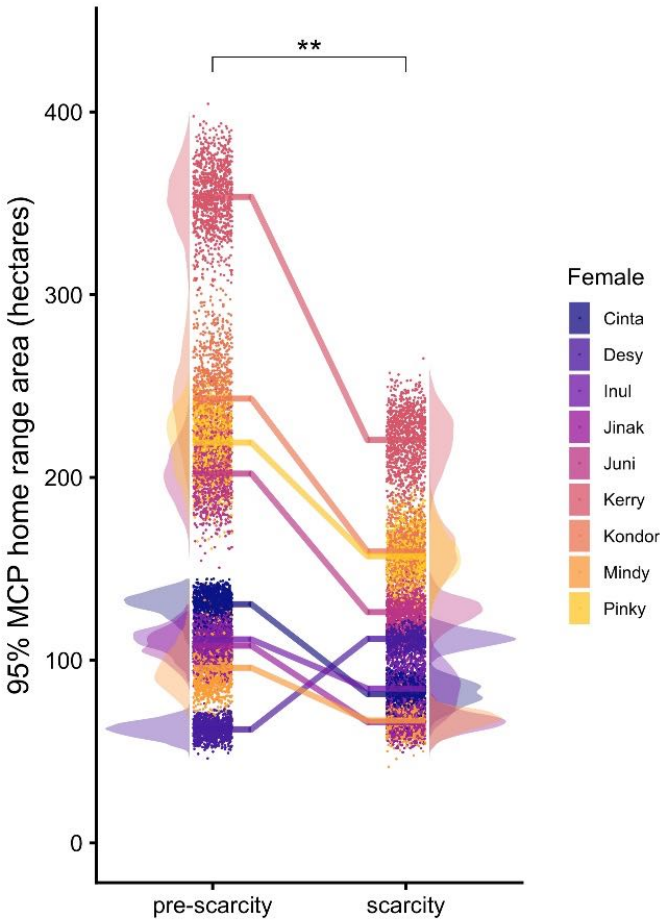

Figure 3.3: The home range areas (in hectares) of each adult female in the pre-scarcity and scarcity periods at Tuanan. Different colours represent the 9 different adult females, and each point represents a single iteration, calculated from 100 randomly selected location points, while the shaded areas represent the density distributions of each individuals' 1000 iterated ranges. Horizontal lines represent individuals' means, with the slope of the connecting line meant to illustrate the degree of change from pre-scarcity to scarcity.

The home ranges of four females overlapped with the area that was burned during the fires. Figure 3.S6 shows the proportion of these females' pre-scarcity and scarcity ranges that were within the burned area. Only one female, Cinta, had a substantial portion (35%) of her home range burned in the fires. Indeed, the size of Cinta's scarcity range (81 ha) is almost exactly equal to the unburned area of her pre-scarcity range (80 ha), suggesting

that her decrease in home range size may simply be because she was avoiding the burned area after the fires. We therefore re-evaluated the linear mixed model including only the 8 other females (i.e. leaving out Cinta), to be sure that the significant decrease in home range size that we had found was not being driven by Cinta's substantial loss of her home range area to the fire. Without Cinta, the mean home range area of the other eight adult females at Tuanan pre-scarcity was 174 hectares (range = 46 to 404 ha, n_{ranges} = 8000, $n_{individuals}$ = 8) and during the scarcity episode was 124 hectares (range = 42 to 265 ha, n_{ranges} = 8000, $n_{individuals}$ = 8). The home range areas remained significantly smaller during the period of fruit scarcity, than they were pre-scarcity, during the period of normal fruit availability (LMM: n_{ranges} = 16000, $n_{individuals}$ = 8, $b \pm SE$ =-50.36 ± 17.59, t = -2.86, p < 0.005).

Identification of adult females on Wehea camera traps

Overall, we collected 362 camera trap records of orangutans. Of these, 106 were determined to potentially be adult females, and of these, 56 records included at least one photo of the face of an adult orangutan. Of these, there were 43 camera trap records of adult female orangutans for which an identity could be assigned. Two records could not be assigned with certainty to a female in the 'split' scenario (the most conservative estimate of female locations, which acknowledges the maximum number of females who may have been recorded), while all 43 were assigned to a female in the 'lumped' scenario (the less conservative but equally plausible estimate of female locations, which acknowledges the minimum number of females who may have been recorded). Table 3.2 gives an overview of the number of records and locations of each identified female in the two scenarios.

In the 'split' scenario, there were 11 unique females identified, each with at least 2 records (median number of records per female = 4, max = 7). Of these 11 females, 2 were each recorded at only one camera trap station (i.e. only one single location), and were therefore excluded from subsequent analysis because no inter-location distance could be measured. In the 'lumped' scenario, there were six unique females identified, each with at least 3 records (median number of records per female = 7, max = 12). All six of these females were recorded at >1 camera trap station, and included in the subsequent analysis. Table 3.S2 gives a detailed overview of each camera trap record that was assigned to a female identity, including the date and time of each record, and the location of the camera trap station. Figure 3.4 shows the locations at which each identified female was recorded in the 'split' and 'lumped' scenarios.

Table 3.2 Overview of female IDs assigned in the 'split' and 'lumped' scenarios and the number of records and unique station locations in/at which each female was recorded at Wehea

	Female ID	No. of records	No. of locations	ID in alternative scenario
Lumped scenario	Janet	7	4	Candy, Pima
	Penelopi	7	5	Aunti, Isidora, Pi
	Rose	3	3	Rose
	Semma	4	2	Semma
	Spice	10	7	Eva, Jackie
	Trixie	12	7	Barbara, Pansy
Split scenario	Auntie	3	1*	Penelopi
	Barbara	4	3	Trixie
	Candy	5	3	Janet
	Eva	5	4	Spice
	Isidora	2	2	Penelopi
	Jackie	4	3	Spice
	Pansy	7	4	Trixie
	Pi	2	2	Penelopi
	Pima	2	1*	Janet
	Rose	3	3	Rose
	Semma	4	2	Semma
	unidentifiable	2	2	Trixie, Spice

* Females recorded at only a single location were excluded from the statistical analysis

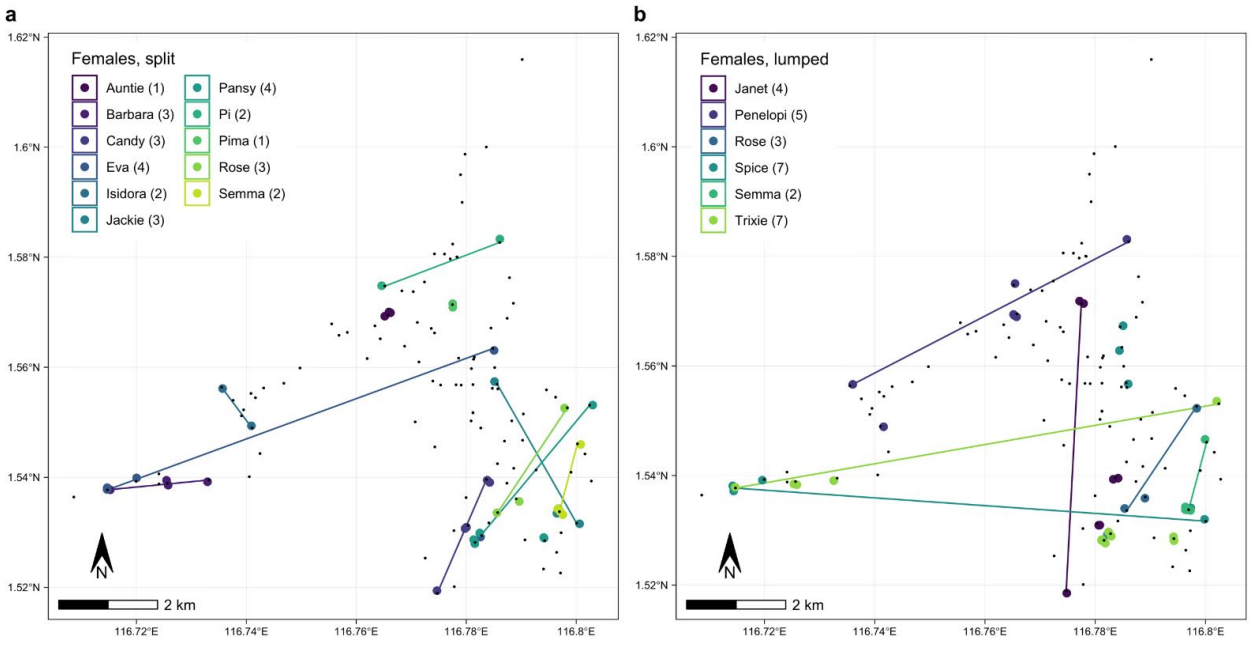

Figure 3.4: The locations at which each identified female was recorded in the split (a) and lumped (b) scenarios on the Wehea camera traps. Note that the females' location points have been jittered slightly, so as to show all points at each single location. The tiny black dots represent camera trap stations, the number after each name in the legend represents the number of different camera trap stations at which that female was recorded, and the lines show each female's maximum inter-location distance.

Wehea vs Tuanan inter-population comparison

'Split' – In the 'split' scenario, the median maximum inter-location distance of females at Wehea was 2492 meters (range = 1023 to 8300 m, mean = 3014 m, n = 9) and the median of each female's average maximum inter-location distance at Tuanan was 695 meters (range = 607 to 944 m, mean = 739, n = 5). The maximum inter-location distances of females at Wehea were significantly longer than those of females at Tuanan (Mann-Whitney U = 45, $p < 0.001$) (Fig. 3.5a). Removing the female with the highest Wehea value (Eva, 8300 meters), yields a median maximum inter-location distance at Wehea of 2487 meters (range = 1023 to 3599 m, mean = 2353, n = 8), and is also significantly higher than Tuanan (Mann-Whitney U = 40, $p < 0.005$). The 95% quantile of all Tuanan maximum inter-location distances from all iterations was 1660 meters (range = 0.1 to 2897 m, mean = 744 m, median = 718 m, $n_{values} = 31647$). Of the 9 Wehea females, 7 had maximum inter-location distances that were above the Tuanan 95% quantile (i.e. that were significantly longer than those at Tuanan) (Fig. 3.5b).

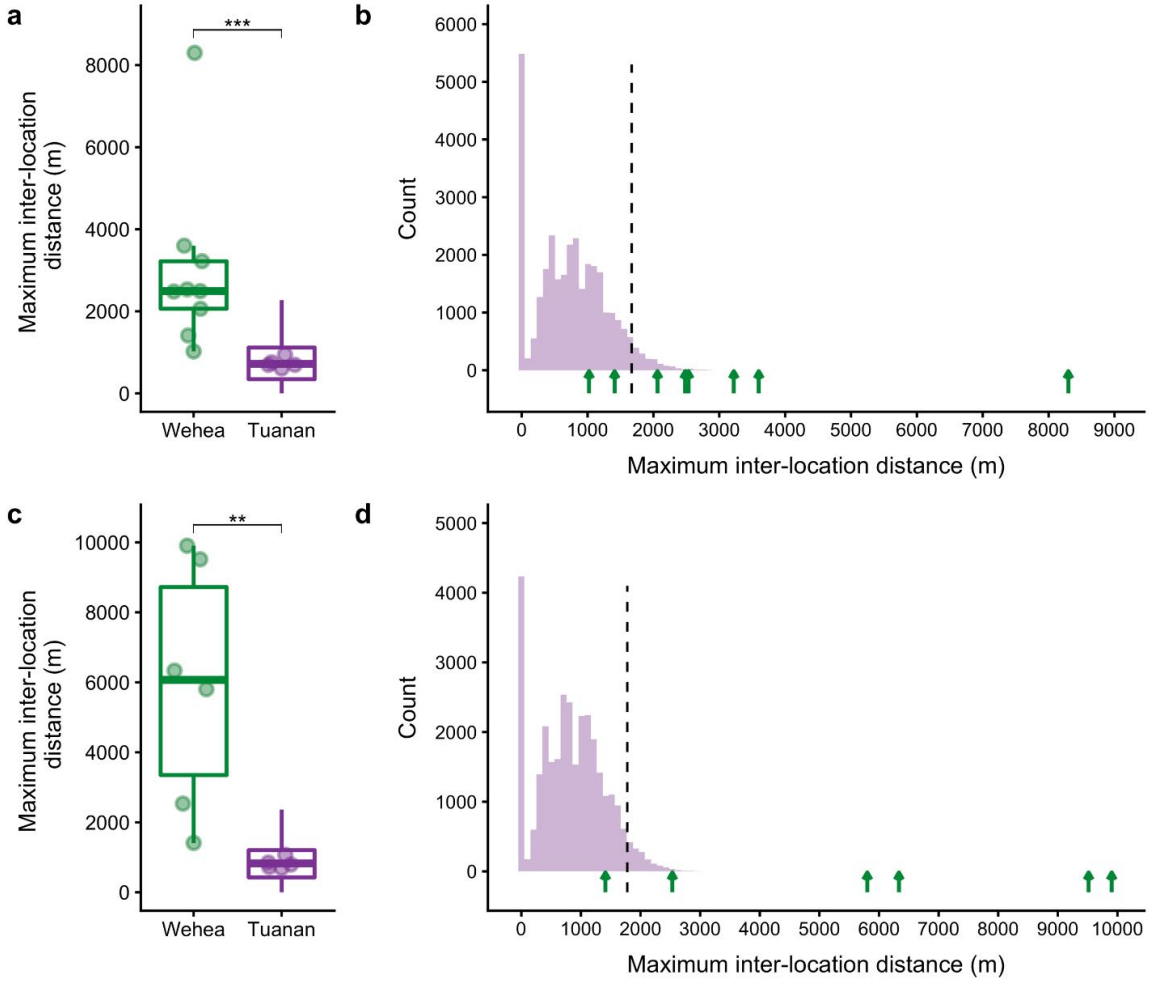

Figure 3.5: The maximum inter-location distances of each adult female in the (a, b) 'split' scenario, and (c, d) 'lumped' scenario. In plots a and c, boxes represent the full datasets (for Tuanan, this includes all iterations), and each point represents one individual (for Tuanan, these are the individual means from all iterations). In plots b and d, the purple histogram represents all maximum inter-location distances from all iterations at Tuanan, the dotted black lines represent the 95% quantile values of the histograms, and the green arrows each represent the maximum inter-location distance of a single female at Wehea. Significance stars refer to the Mann-Whitney U tests between the Wehea females' values and Tuanan females' mean (over all iterations) values.

'Lumped'– In the 'lumped' scenario, the median maximum inter-location distance of females at Wehea was 6069 meters (range = 1411 to 9904 m, mean = 5917 m, n = 6) and the median of each female's average maximum inter-location distance at Tuanan was 796 meters (range = 693 to 1069 m, mean = 826, n = 5). The maximum inter-location distances of females at Wehea were significantly longer than those of females at Tuanan (Mann-Whitney $U = 30$, $p < 0.005$) (Fig. 3.5c). The 95% quantile of all Tuanan maximum inter-location distances from all iterations was 1761 meters (range = 0.1 to 3081 m, mean = 839 m, median = 825 m, n_{values} = 31217). Of the 6 Wehea females, five had maximum inter-location distances that were above the Tuanan 95% quantile (i.e. that were significantly longer than those at Tuanan) (Fig. 3.5d).

DISCUSSION

Our results show that female orangutans living in the peat-swamp forest of Tuanan have significantly smaller home ranges during a period of uncharacteristically prolonged low fruit availability. This suggests that they are employing a dietary response to this scarcity episode, incorporating more ubiquitous fallback foods into their diets, and contracting their ranges accordingly. Orangutans exhibit great dietary plasticity, and diet-switching in response to scarcity has been documented extensively (e.g. Morrogh-Bernard et al. 2009; Vogel et al. 2009; Bastian et al. 2010; Campbell-Smith et al. 2011) – thus, this response is expected.

In contrast, the comparison between Wehea and Tuanan strongly suggests that female orangutans at Wehea – who experience long-term fruit scarcity between dipterocarp masting events – may rely on an entirely different ecological strategy for coping with scarcity: they are likely be employing a ranging response, travelling long distances in search of fruit and/or higher quality fallback foods. This is supported by our evidence of individual female orangutans at Wehea being recorded in locations that are significantly farther apart than locations at which individual female Tuanan orangutans have been observed, and indeed, to our knowledge, farther apart than any locations ever reported for individual female orangutans (over 8 km), even in our most conservative – the 'split' – scenario.

Ranging versus dietary responses

This evidence of a strong ranging response to scarcity at Wehea suggests that our predicted criteria under which some degree of area-switching would occur are correct. First, for a ranging response as drastic as area-switching to be necessitated, the scarcity episode must be severe and long enough that locally available fallback foods are either not available or are insufficient. At Wehea, in between masting events, the percentage of fruit-bearing trees in marked plots has been measured at as low as zero (SNS and R. Delgado, unpublished data; Fig. 3.2), and there is no clear evidence of any high-quality and widely available fallback foods (AMA, personal observation). Direct observation suggests that, when fruit is scarce at Wehea, orangutans rely on widely-dispersed unripe fruit (AMA and SNS, unpublished data) – thus a ranging response, namely moving through a huge area and/or switching between areas, is required in order to locate this unripe fruit. At Tuanan, on the other hand, fruit availability does fluctuate, but in a much more predictable pattern and scarce periods usually only last for a few months. Furthermore, the Tuanan habitat contains a high-quality fallback food which is consistent it its spatial and temporal availability: the leaves and fruits and flowers of the kamunda vine (*Leucomphalos*

callicarpus) (Meric de Bellefon et al., in prep). Thus, during periods of scarcity at Tuanan, a dietary response is less risky than a ranging response.

Second, area-switching is only possible where an animal can move to a new habitat, and can do so without incurring high energetic costs. Wehea and Tuanan differ in this respect in two primary ways: 1) the habitat grain, and 2) female orangutans' propensity for energetically low-cost ground travel. First, the Wehea habitat has extreme topographic variation – it is a mesh of high ridges and steep ravines – and therefore has a fine grain of variation in plant taxa and phenology. At Tuanan, on the other hand, the forest is generally very homogeneous, with only a weak gradient of increasing peat depth toward the east, and orangutans would need to travel far to access phenologically asynchronous habitat. Secondly, at Wehea, orangutans – including adult female orangutans – have been shown to use the ground extensively, especially old logging roads (Loken et al. 2013; Loken et al. 2015), and orangutans are generally able to travel faster and more cryptically on the ground than through the trees (Ashbury et al. 2015). Female orangutans are captured on ground-level camera traps more often at Wehea than at Tuanan, suggesting that female orangutans at Wehea are making more use of this low-cost method of travel than at Tuanan (Loken et al. 2013; Ashbury et al. 2015). Together, this fine-scale habitat variability combined with low-cost travel may mean that – in terms of exploring a wide area in search of phenologically asynchronous habitat – the ratio of potential energetic risks to rewards at Wehea is less than at Tuanan, thus facilitating a ranging response to scarcity at Wehea.

Lastly, we expect that animals will area-switch only when the costs associated with ranging in the new habitat are low, and outweighed by the potential benefits. For orangutans, who have few natural arboreal predators (aside from humans) these potential costs would be primarily social. At Wehea, the population density is extremely low and associations between adult females are rare (AMA and SNS, unpublished data), suggesting that there is 'space' for females to move through the habitat and settle locally in different areas over time, without incurring high costs of social aggression or feeding competition. Tuanan, on the other hand, has the highest population density of wild Bornean orangutans on record (van Schaik et al. 2005), and aggression between females is not uncommon (Marzec et al. 2016, Ashbury et al. under review) – especially during times of scarcity (Meric de Bellefon et al. in prep) – suggesting that the social landscape would not be conducive to a ranging response such as area-switching: there is no 'open space' for females to move into, and widely ranging females risk being met with hostility. Thus, as expected, at Tuanan we see strong evidence of diet-switching with a corresponding shrinking in home range size, rather than area-switching or a home range expansion.

It is important to note that our method of data collection at Wehea, namely camera trapping, is likely to underestimate the extent of female orangutan space-use, relative to studies based on long-term extensive direct observation of focal followed females for three primary reasons: 1) the potential area over which an orangutan can be recorded is limited by camera trap placement – in our case, this means that any females who move into areas beyond our camera trap network have no chance of being recorded; 2) even if an area is monitored by a camera trap station, and a female does pass through that area, she is not guaranteed to be recorded – if she is moving through the canopy where there is a ground-level station, or if she passes the station out of range of the camera trap sensors, she will not be photographed; and 3) even if a female is photographed by a camera trap station, if the photo is unclear or does not capture her face, then she would not be identified. All of these factors

suggest that the true spatial extent of each individual female's movement at Wehea could be substantially wider than we have recorded. In contrast, at Tuanan (or other sites using direct observation methods) females are subject to focal follows on a regular basis and would be followed by observers into new areas and/or far-reaching parts of their home ranges, if such behavior occurs. Hence, maximum estimates from long-term direct observation studies are more certain.

Central Bornean orangutans living in mosaic habitats, have female home range sizes of up to 600 (Tanjung Putting, Galdikas 1988) or 800 (Gunung Palung, Knott 2008) hectares. While our methods at Wehea do not allow us to calculate polygon home ranges and these studies of female orangutans in mosaic habitats do not report on the maximum inter-location distance of individuals, maps in Knott et al.'s (2008) report of female home ranges in the mosaic habitat of Gunung Palung indicate that the home range polygon shapes are generally equal in their north-south and east-west length, suggesting that the maximum inter-location distance of a female with an 800-ha home range is approximately 3'190 meters (the diameter of a 800-ha circle). This is within the range of individuals' inter-location distances in our more conservative, 'split,' scenario, but still at the lower end of our range of individuals' inter-location distances in our equally-probable 'lumped' scenario. At Suaq Balimbing, in a population of Sumatran orangutans living in a mosaic habitat, females had maximum inter-location distances of up to 4.5 kilometers, measuring from all follow data over a 4-year period including even one-time excursions outside of their frequently used areas (Singleton and van Schaik 2001). This is towards the high end of our 'split' scenario measurements, and within the mid-range of our 'lumped' scenario measurements at Wehea. However, measuring maximum inter-location distances at Suaq of only frequently used areas would yield a measurement of less than 2.5 kilometers (based on a visual assessment of the maps provided in Singleton and van Schaik 2001). This is at the low end of our 'split' and 'lumped' scenario estimates for Wehea.

Even where inter-location distances of female home ranges in mosaic habitats are within the range of inter-location distance estimates at Wehea, some Wehea females' distances are significantly farther (especially in the 'lumped' scenario) despite using this method that should underestimate distances. We therefore believe this is strongly suggestive of some degree of area-switching, or at least uniquely vast home ranges, among the orangutans at Wehea. Based on our data collection methods at Wehea, it is not possible to precisely determine where, on the ranging response spectrum, these females' ranging patterns fall; what we are observing at Wehea could be evidence of a very extreme area-switching response wherein females are leaving their regular home ranges and moving out into totally different, detached, areas. Alternatively, we could be seeing evidence of a general reduction in site-fidelity, with females moving over vast ranges which – with enough data – may yield measurable home ranges.

There is some evidence from preliminary behavioral focal follows of a well-habituated adult female orangutan at Wehea (AMA and SNS, unpublished data) which is strongly suggestive of area-switching: adult female Pi was observed in the 1200-hectare direct observation study area regularly (during 10 out of 20 observation months) when fruit availability was high (masting) and medium (post-mast) between May 2014 and May 2016. However, once fruit availability had dropped very low again (starting after May 2016), she was not observed again during the remaining 12 months of the study, despite extensive search effort. This pattern of observation suggests that, while Pi had a measurable home range of approximately 350-hectares within the study area, she

completely abandoned this home range when fruit availability in this area plummeted. While this range-use data concerns just one single female, it is strongly indicative of area-switching, thus suggesting that female orangutans at Wehea are not simply maintaining large home ranges, but are using and abandoning areas altogether depending on the spatiotemporal distribution of fruit.

Such a within-species, between-population, qualitative contrast in response to fruit scarcity, as we see here among Bornean orangutans, is rare. Among chimpanzees, there is variation in the foods and feeding techniques to which different populations diet-switch during periods of fruit scarcity; for example, the Bossou chimps in Guinea, West Africa, incorporate three fallback foods into their diets when ripe fruit is scarce, two of which – oil-palm nuts and pith – require tool-use (nut-cracking and pestle-pounding) (Yamakoshi 1998), while chimps living in the Goualougo Triangle study area in the Republic of Congo diet-switch to leaves (which require no tool-use) (Sanz and Morgan 2013), whereas chimps living in the small forest fragments in a cultivated landscape in Uganda diet-switch to foods obtained through crop raiding when forest fruit is low (McLennan 2013). There is no clear evidence of area-switching or a strong ranging response to preferred food scarcity among any population of chimpanzees, though there is evidence that chimpanzees living in mosaic landscapes move between different habitat types within already-established home ranges (e.g. Furuichi et al. 2001a; Furuichi et al. 2001b). Perhaps the strict territoriality of chimpanzees, with potentially lethal altercations between neighboring communities (Wilson and Wrangham 2003; Wilson et al. 2004), makes area-switching virtually impossible. The alternative, then, is to establish exceptionally large home ranges incorporating several habitat types. Indeed, chimpanzees at Fongoli, who live in a hot, dry savanna mosaic habitat, maintain such large ranges, and they spend more time than expected in forest patches – where water sources are continuously available – especially during the dry season (Pruetz and Bertolani 2009). These larger ranges in the context of a harsher environment, as observed at Fongoli, may be functionally similar to what we are observing at Wehea among orangutans.

Geographic variation in female orangutan space-use

Our results stand in stark contrast to those reported previously for female Northeast Bornean orangutan (*P. p. morio*) home range sizes. Studies of female orangutan home ranges have consistently reported the smallest home range sizes among this subspecies of orangutans: 40 to 180 hectares (Singleton et al. 2009), and have not given any indication that females may move through wider areas, or area-switch out of these small home ranges during times of scarcity. Rather, past studies have concluded that female Northeast Bornean orangutans live in small home ranges and switch to bark and other ubiquitous low-quality fallback foods during times of scarcity (Morrogh-Bernard et al. 2009). We therefore suggest two possible explanation for our contrasting results: 1) Wehea may be an anomaly, and the expanded ranging of these females may be unique to this population/habitat; or 2) previous studies of Northeast Bornean orangutans may not have captured the full extent of their ranging patterns due to the limited duration of studies.

It is possible that the orangutans of Wehea are indeed an anomaly when compared to other populations of Northeast Bornean orangutans, as this subspecies exhibits particular adaptations for coping with scarcity – namely, smaller brain size (Taylor and van Schaik 2007), and more robust jaw morphology (Taylor 2006) – that would indicate an evolutionary preference for diet-switching to lower quality and more difficult to process

fallback foods (Taylor 2009; Vogel et al. 2014). Indeed, Russon et al. (2015) discuss the resilience and dietary flexibility of Northeast Bornean orangutans in Kutai National Park after the 1997-1998 drought and forest fires caused significant changes to their habitat's structure and phenology; orangutans exhibited multiple, ongoing, adjustments to their diet as the forest regenerated. These dietary adjustments (some facilitated by the aforementioned morphological adaptations to fallback food consumption) do not, however, preclude a ranging response to scarcity, nor are dietary and ranging responses mutually exclusive strategies. It is possible that orangutans at Wehea may engage in some degree of area-switching in search of higher-quality fallback foods (such as unripe fruit), until the degree and duration of fruit scarcity is such that they are required to diet-switch to more difficult-to-process fallback foods such as woody vegetation and inner tree bark.

It is also possible that previous studies of Northeast Bornean orangutans have not recorded the full extent of female ranging patterns in these populations. Compared to studies of Central Bornean orangutans, studies of Northeast Bornean orangutans have been mostly short in duration (up to 48 months) or researcher presence was sporadic over time, and the studies took place in relatively small study areas (up to 600 hectares) (Singleton and van Schaik 2001; Singleton et al. 2009). These studies may have therefore measured home ranges that represent only seasonal or temporary ranges, or small portions of larger ranges. Indeed, there is emerging evidence from the Bendili site in Kutai National Park (Russon et al. 2015) that female Northeast Bornean orangutans in this population have home ranges that are significantly larger than the 40 to 180-hectares previously estimated in the same general area by Rodman (1988), Mitani (1989), and Suzuki (1992): individually-identified female orangutans have been observed at two separate research camps, which are over 4.5 kilometers apart (A. Russon, personal communication). These observations at Kutai suggest that wide-scale ranging of female Northeast Bornean orangutans, such as we have observed at Wehea, may be more common than previously thought.

Comparative studies of female orangutan space-use have also consistently shown that habitat heterogeneity can explain a large degree of the variation in female home range size: females living in more heterogeneous habitats have larger ranges, as they maintain access to different habitat types in their local mosaic (Singleton and van Schaik 2001; Singleton et al. 2009). Furthermore, Kanamori et al (2016) at Danum Valley and Buij et al. (2002) at Ketambe, present evidence of seasonal fluctuations in orangutan population densities which correlated with seasonal fluctuations in local fruit availabilities. They suggest that these population fluctuations result from orangutans moving around within large home ranges in heterogeneous habitats in search of fruit (Buij et al. 2002; Kanamori et al. 2016). As far as we are aware, however, there are no published studies which have presented evidence that is so strongly suggestive of potential area-switching among individually-identified orangutans, such as what we have observed at Wehea.

Implications

The long-distance ranging of female orangutans at Wehea may have strong implications for culture and cognition among this population. Across the geographic range of wild orangutans, it has been shown that habitat productivity correlates with gregariousness, and that this gregariousness leads to larger learned skill repertoires among individual orangutans and larger population cultural repertoires (van Schaik et al. 2009; Schuppli et al. 2017). In order for innovations to subsist in orangutan populations, they need to be passed among individuals through close-proximity social learning (Schuppli et al. 2016). There is evidence that tolerant associations –

especially between adult females – occur primarily between predictable, regular, social partners, such as maternally related females who live in overlapping home ranges (van Noordwijk et al. 2012; Marzec et al. 2016). Furthermore, it has been shown that immature orangutans benefit greatly from the sociality of their mothers, with associations between mothers and other conspecifics providing offspring with social play partners and social learning opportunities (van Noordwijk et al. 2012; Schuppli et al. 2016), and immatures showing increased evidence of socially-mediated skill learning after close-range observation of familiar, usually related, conspecifics, rather than strangers (C. Schuppli, unpublished data). The exceptionally low population density at Wehea, combined with the long-distance ranging among females, likely leads to not only limited gregariousness, but also limited stability and predictability in potential social partners. This lack of familiarity with one's nearby conspecifics may limit social tolerance and thus limit opportunities for social learning and cognitive skill development among the orangutans at Wehea.

Our results also have important implications for orangutan conservation, especially with respect to landscape planning. Our study highlights the variability in orangutans' responses to scarcity, and the fact that, in contrast to what was previously assumed, orangutans are likely to employ a ranging response – marked by wider roaming and possibly area-switching – in habitats with notably low and inconsistent fruit productivity. It is therefore clear from our study that forest connectivity is of the utmost importance for conserving orangutans. Nest surveys have suggested that substantial Northeast Bornean orangutan populations occur in human-altered landscapes dominated by oil palm or pulp and paper plantation concessions (Spehar and Rayadin 2017). However, the degree to which these orangutans are moving through such habitats and to which they depend on surrounding, less-disturbed habitats, is unknown. Our results suggest that orangutans nesting in industrial plantations may be just 'passing through' on their way between alternative habitats, rather than settling and establishing sustainable home ranges within these plantations. Indeed, Rayadin and Spehar (2015) showed body-mass evidence that some orangutans living in oil palm and forestry plantations were experiencing extreme energetic stress, including those individuals who had access to natural forest patches. This all suggests that orangutans would benefit from landscape planning which maintains forest connectivity through plantations, maintaining natural habitat across wider spatial-scales in order to allow orangutans access to variable habitat which may provide asynchronous resources. Furthermore, our results highlight the overall importance of understanding the behavior and ecology of an animal in order to design effective conservation strategies.

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SUPPLEMENTARY MATERIALS

Supplementary Methods

1: Wehea data preparation for inter-population comparison

In order to assign IDs to the camera trap records in the least biased way possible, two independent observers assigned IDs to the orangutans in the photos using a 'blind' method. To achieve this 'blind' ID process, a computer algorithm first processed all records of orangutans as follows: 1) Each record was given a unique random number ("record number"), 2) Each photo within a record was numbered in the sequence in which it was taken ("photo number"), 3) These record-photo numbers of each photo were saved in a table with the metadata of each photo, including the date and time, the station name, and the location of the camera, 4) Any visible metadata on the photos themselves were removed (i.e. the top and bottom strip, containing the date, time, and station ID of the photo/camera were cropped from the photos), and any metadata within the photo file data was deleted, 5) The photo file itself was renamed with its unique record-photo number, 6) The record numbers were stored in a table with the years that each record was captured, and 7) The year column was blanked out, and so knowing the year that a record was captured required deliberate checking.

One experienced observer (AMA) then sorted through all of the photos and extracted all records of adult females with and without offspring, wherein the orangutans' faces were visible. Two experienced observers (AMA and SNS) then each, independently (without consulting each other or the original photo metadata), went through all photos of all adult female records, and grouped them together into likely individuals. Both observers assigned an ID and a level of certainty regarding that ID between 1 and 3 (1 – not very sure, 2 – probably, 3 – very certain) to each record. IDs were assigned based primarily on facial characteristics, such as the shape of the face, eyes, and nostrils, the shape of the hairline and the thickness of the forehead and head hair, and the prominence and orientation of the cheekbones. In some cases, offspring size and facial characteristics were used to verify the probability of an ID – in these cases, it was possible for observers to check the year that a record was captured, in order to account for the growth and development of these dependent offspring.

The IDs and certainty levels of AMA and SNS were then amalgamated into a single table of all records. Records in which the IDs of AMA and SNS were not in agreement and at least one observer had low (0 or 1) level certainty of their ID were discarded. The records which we retained for the analysis were therefore those in which AMA and SNS either agreed in their IDs, or AMA and SNS disagreed but both had relatively high (2 or 3) levels of certainty. In all cases where AMA and SNS disagreed and both had high levels of certainty, it was a case of one observer having 'split' records into 2 individuals where the other observer had 'lumped' these same records under a single individual. We therefore assigned 2 possible IDs to each camera trap record: a 'split' ID and a 'lumped' ID. The 'split' ID represents the more conservative estimates of female IDs and locations: where at least one observer 'split' a group of records into 2 different individuals, the IDs of those photos are split, thus decreasing the likelihood of each individual female being recorded at multiple locations. The 'lumped' IDs, however, represent less conservative estimates of female IDs: where at least one observer 'lumped' a group of records under a single individual, the IDs of those photos are lumped, thus increasing the likelihood of each individual female being recorded at multiple locations.

In the end, therefore, we had two datasets – a 'split' dataset and a 'lumped' dataset – each consisting of a list of camera trap records and their female IDs, which could then be re-associated with the photos' metadata, including the date and time, and the camera trap stations at which the record was captured. Figure 3.S3 shows an example of five camera trap records and their associated IDs in the 'split' and the 'lumped' scenario.

2: Tuanan data preparation for inter-population comparison

In order to obtain estimates of these females' space-use that were comparable between Wehea and Tuanan, despite the difference in data collection methods, we used a process of iterations and sub-setting applied to the Tuanan location (collected during focal follows) in such a way that its output would mimic the Wehea data (collected from camera traps).

First, the core area (i.e. the 50% minimum convex polygon, MCP) of all 5 females' location points was calculated – henceforth referred to as the 'total female 50% MCP'. Next, the map of the camera trap station locations at Wehea was 'moved' – maintaining the spatial configuration, relative inter-station distances, etc, of the camera trap stations – and superimposed over the Tuanan study area. Next, in 10,000 iterations, the following procedure was conducted (see Figure 3.S4a – g for visual depictions of the process):

1) A random X and Y shift, and a random angle of rotation between 0 and 359 degrees, was added or subtracted from the camera trap map (so that the spatial configuration of the camera trap stations was maintained, but its position within/relative to the Tuanan study area was changed) (Fig. 3.S4b).
2) This superimposed camera trap map was checked to ensure that at least one camera trap station location fell within the total female 50% MCP, i.e. to be sure that the camera trap map did overlay the area wherein the Tuanan females ranged – if it did not, then step 1 and 2 were repeated (without counting an iteration), and if it did, then the procedure continued to step 3, and counted as an iteration.
3) A 10-meter diameter buffer was put around each camera trap station location (Fig. 3.S4c & d).
4) All female location points (collected during focal follows) that fell within any camera's buffer were extracted (Fig. 3.S4e).
5) For each female, a random number of these extracted points (between 2 and 7 in the 'split' comparison scenario, Fig. 3.S4f, and between 3 and 12 in the 'lumped' comparison scenario, Fig. 3.S4g), or all points if there were 2 or fewer ('split') or 3 or fewer ('lumped'), were randomly selected. The number of extracted points are based on the number of location points obtained per identified female in the Wehea datasets (see Results).
6) Each extracted point was assigned the location of the associated superimposed camera trap station.
7) These two datasets – a 'split' comparative set with up to 7 points per female, and a 'lumped' comparative set with up to 12 points per female – were saved, and the next iteration began.

Thus, essentially, we simulated having the same spatial configuration of camera traps set up at Tuanan as we had at Wehea, and assumed that if an orangutan was located within 10 meters of a camera trap station, that she could be "photographed" by a camera. To keep sample sizes similar between the Wehea dataset and these Tuanan datasets (and to mimic the fact that a female would not necessarily be photographed by a camera trap station simply because she passed within 10 meters of it), we only used a random subset of each Tuanan

female's "photographs", matching the 'records per female' sample sizes obtained for each Wehea female orangutan, in each of the 'split' and 'lumped' scenarios. This process was repeated 10,000 times, with the camera trap map in different positions and at different angles relative to the Tuanan map, but always positioned in such a way that there was relatively high probability that a Tuanan female would be "photographed." Figure 3.S4f & g shows an example of the locations of Tuanan female's "photographs"/records from a single iteration in each of the 'split' and 'lumped' scenarios.

Supplementary Figures

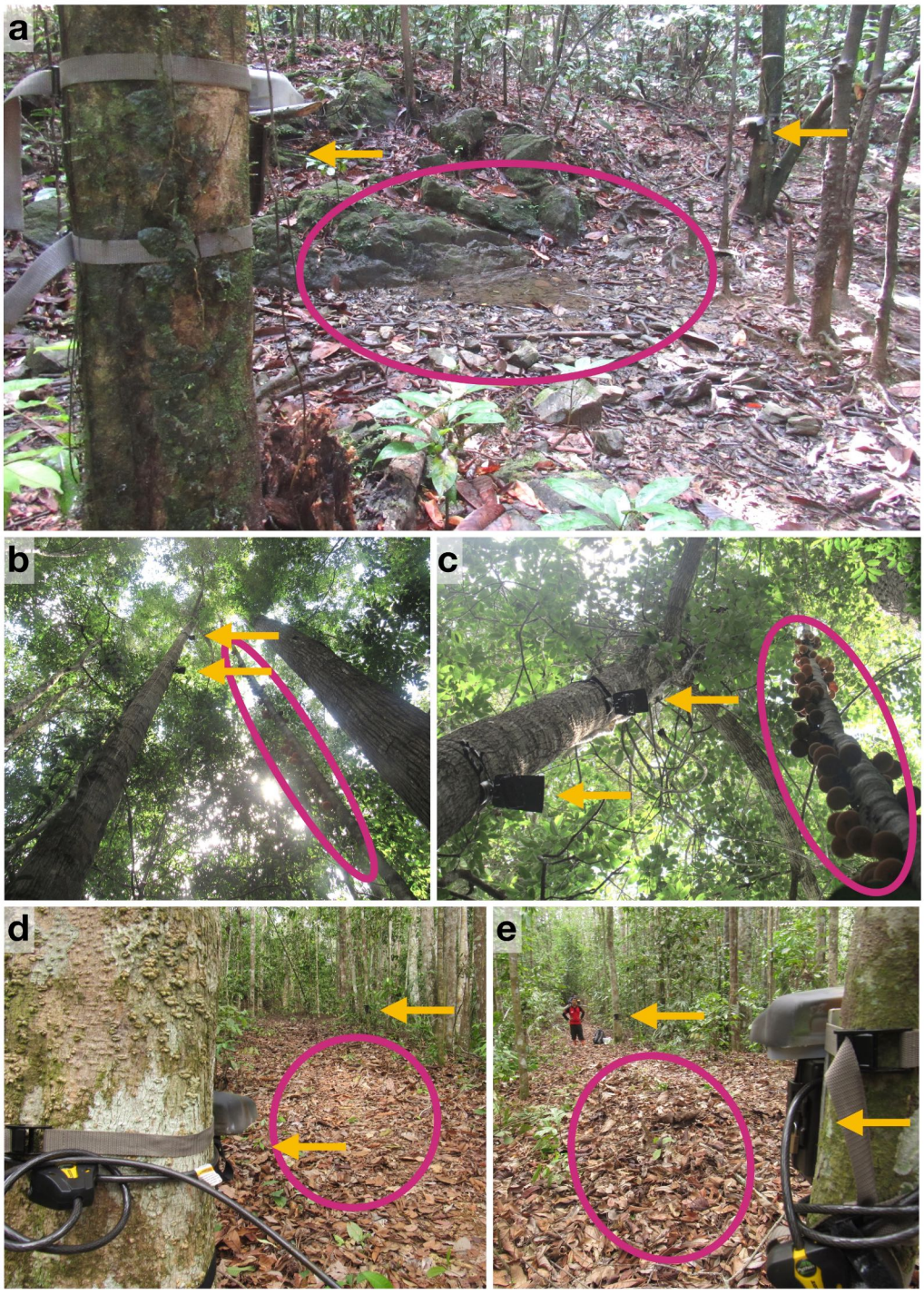

Figure 3.S1: Examples of 3 camera trapping stations during Phase 3 of Wehea data collection. In each photo, yellow arrows point to the camera traps and pink circles indicate the approximate target area of the camera traps. Two camera traps at the Butterfly Sepan station (a) point towards the most active area of the salt-lick, two cameras at the Zone 7 secondary (arboreal) station (b, c) point towards a fruiting *Ficus* vine, and two cameras at the Zone 6 primary station (d, e) point towards each other accross a ridge-line trail.

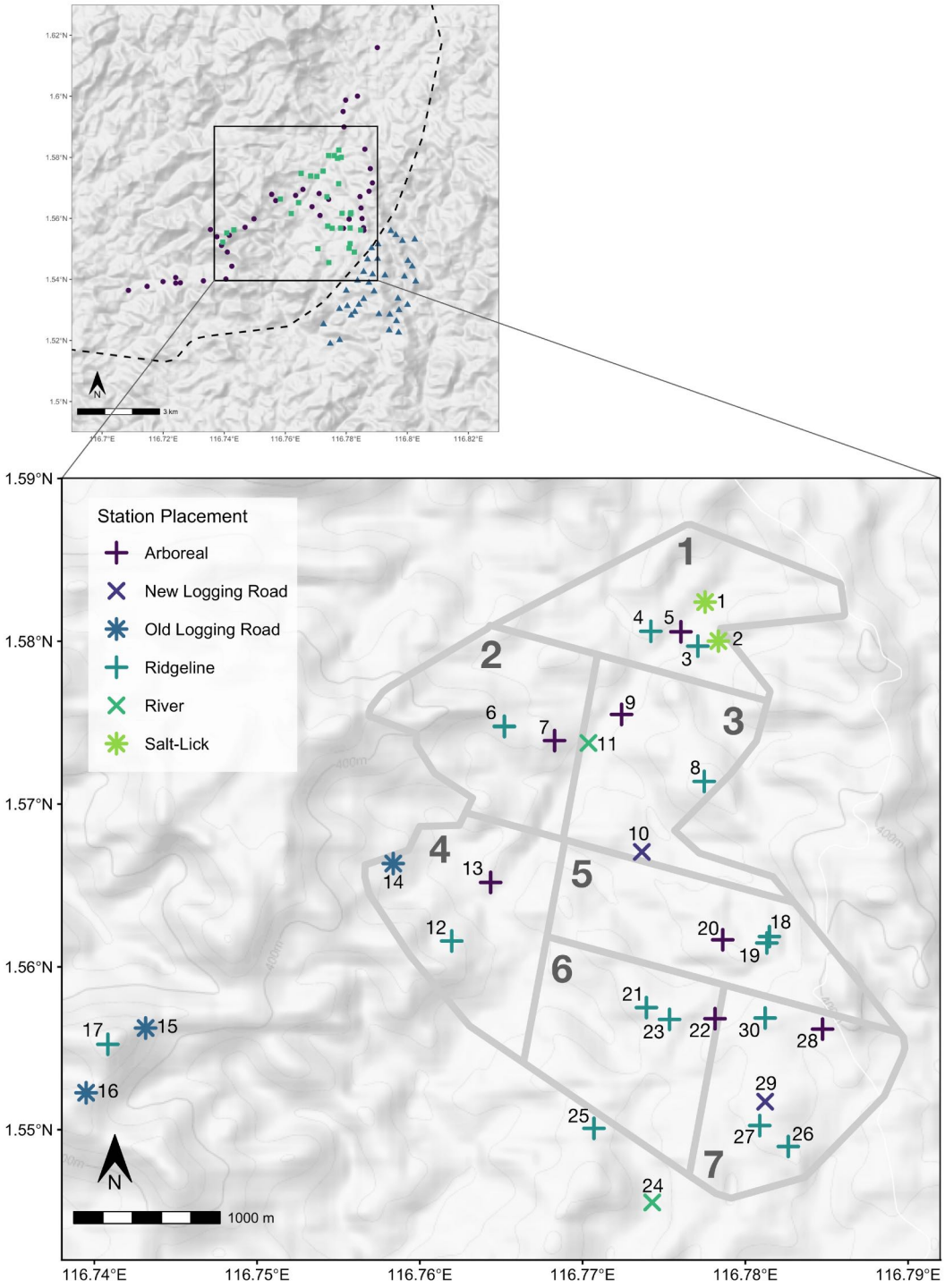

Figure 3.S2: shows the placement of the camera trap stations during Phase 3 of camera trapping at Wehea. The thick light grey lines show the approximate outlines of the seven 'zones.' Large dark grey numbers are the number of each zone and the smaller black numbers are the number of each station – these numbers correspond to the *Map No.* column in Table 3.S1.

Figure 3.S3: Example photos from five different camera trap records in which the female was assigned a definite ID. In the 'lumped' scenario, all 5 records (a – e) are Trixie, while in the 'split' scenario the first two (a, b) are Barbara, and the last three (c – e) are Pansy. Note the absence of the clinging infant in a and b (2012), and the presence of the clinging infant in c – e (2013) (very difficult to see in d), also the similarity in appearance between the offspring in a and b and the older juvenile in e; chronologically, it follows that – if this is the same female in all photos (i.e. Trixie, 'lumped' scenario) – she gave birth to a new offspring sometime in late 2012 or early 2013, but continued to spend time with her older offspring in 2013. These photos have been cropped and their brightness has been adjusted in order to maximize the clarity of the subjects' facial features.

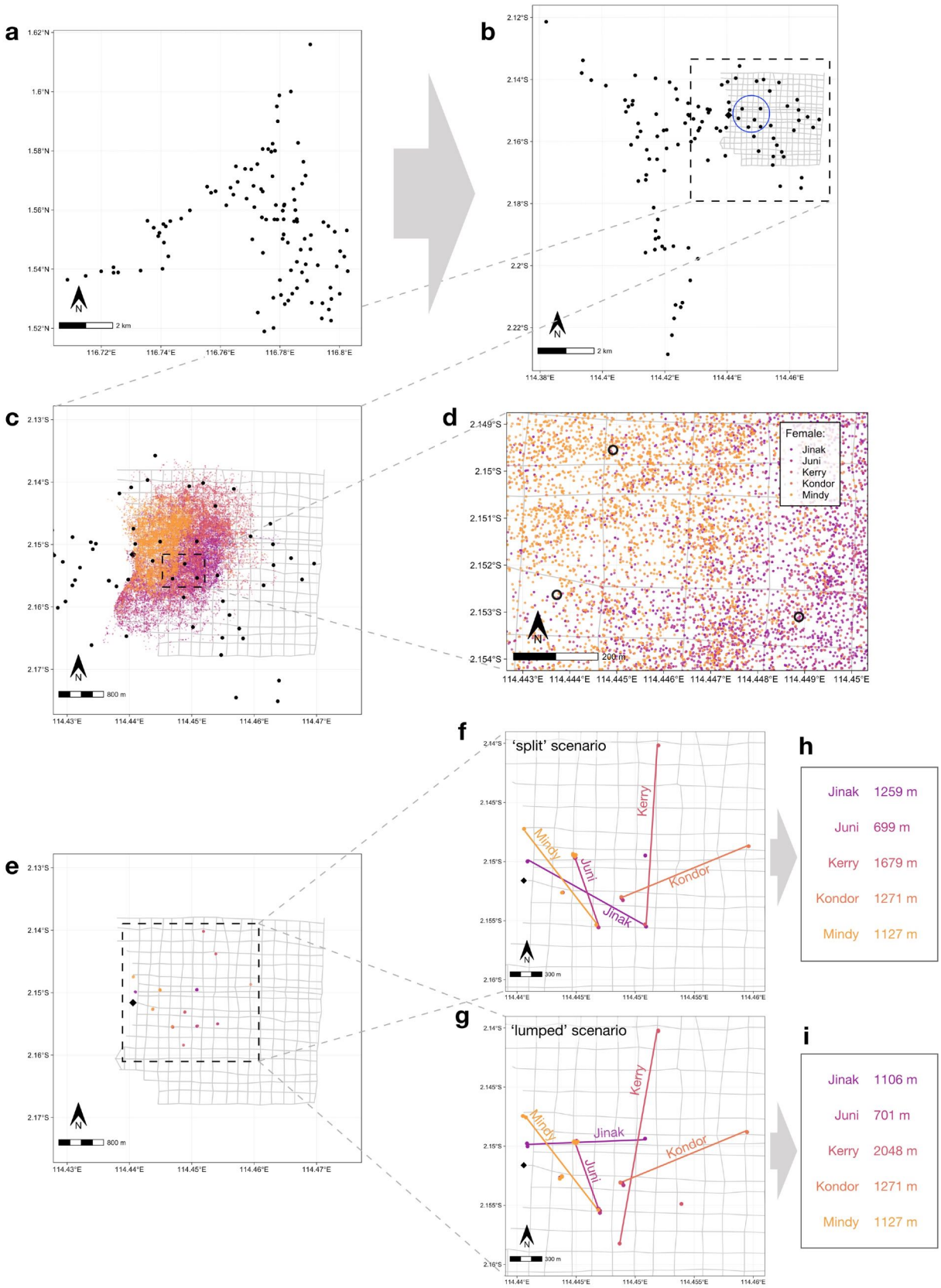

Figure 3.S4: A graphical depiction of a single iteration of the steps used to prepare the Tuanan female location data for the inter-population comparison with Wehea. The camera trap station locations and configuration at Wehea (a) were first superimposed over the Tuanan study area, and then a random X and Y shift and a random angle of rotation was added to the camera trap station map (b), so as to keep the same inter-camera configuration but have it placed randomly over the Tuanan study area. Only iterations in which at least one camera trap station was within the core area (50% MCP) of all five females' location points (blue circle) counted towards the 10,000 iterations. Next, a 10-meter diameter buffer was put around each

camera trap station (c and d) and all female location points within those buffers were extracted (e). Then, for the 'split' scenario (f), 2 to 7 of each females' location points were extracted. For the 'lumped' scenario (g), 3 to 12 of each females' location points were extracted. The coordinates of each extracted point were reassigned to the coordinates of the simulated camera trap station which 'recorded' it. Note that in maps f and g, the location points have been jittered slightly, so as to show all points at each location. After all iterations were completed, the maximum inter-location distances for each female, in each of the 2 scenarios, in each iteration, were measured (f, h and g, i).

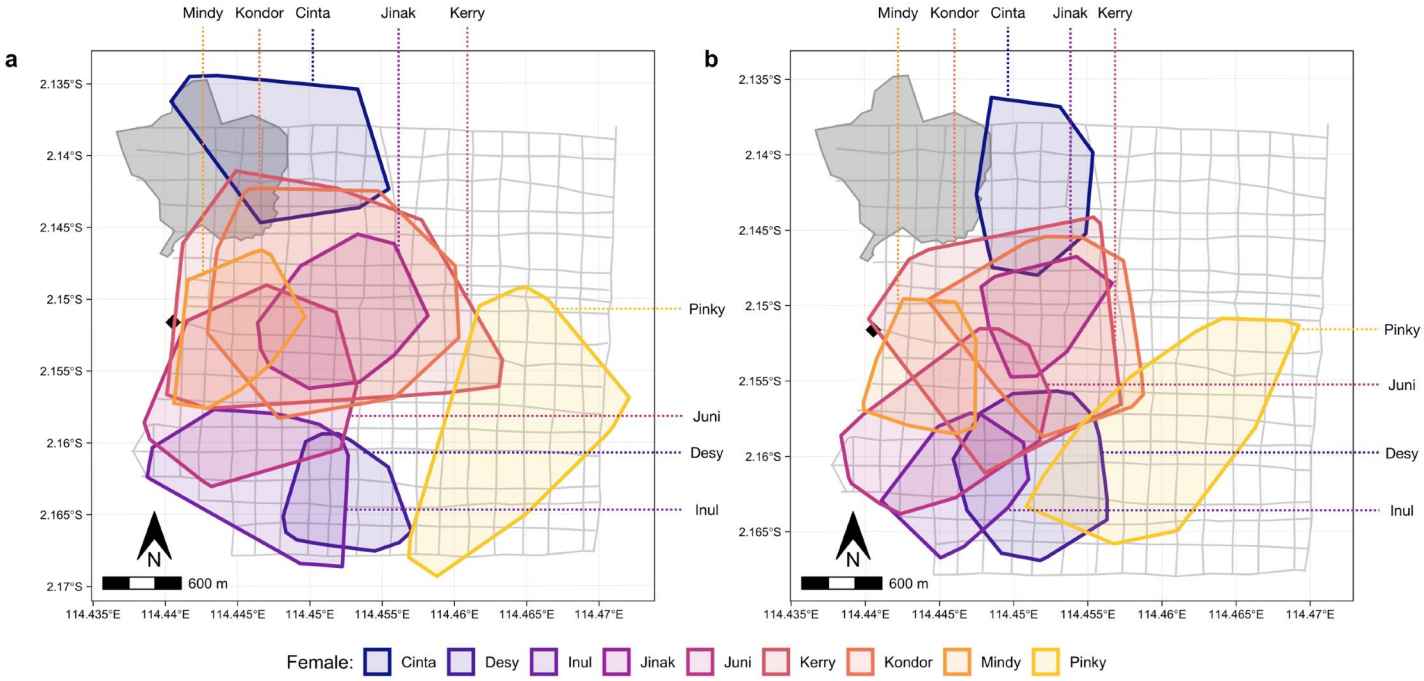

Figure 3.S5: An example of one "pre-scarcity" – Nov 2013 to Oct 2015 (a), and one "scarcity" – Nov 2015 to Sept 2017 (b), iteration of female's 95% MCP ranges at Tuanan. The grey area in the north-west corner shows the area burned between July and October 2015, and the gray lines show the Tuanan study area trail system.

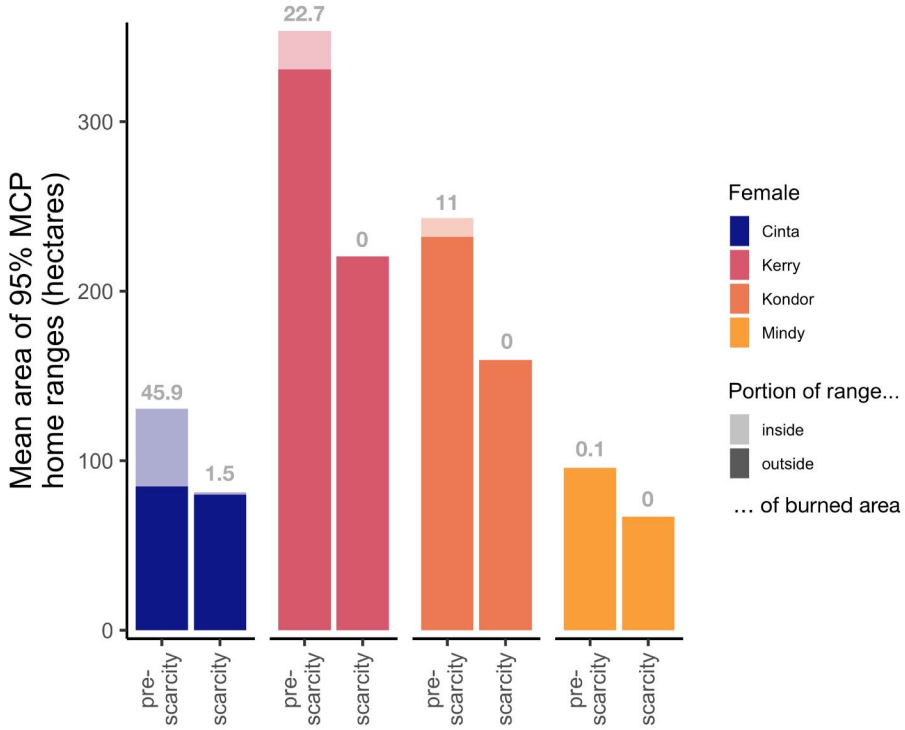

Figure 3.S6: The mean (across iterations) 95% home range areas (top of bar), and the portion that was inside (lighter shade) or outside (darker shade) of the area that was burned by the fires, for the 4 females whose ranges incorporated a non-zero portion of the burned area. Numbers on top of the bars are the mean number of hectares inside the burned area (i.e. the size of the shaded areas).

Supplementary Tables

Table 3.S1 A detailed overview of the camera trap stations at Wehea

Phase	General Location	Station	Map No.[a]	Longitude	Latitude	Elevation	Placement	Start Date	End Date	Active Days[b]
1	Wehea Protected Forest	Large Sepan	*NA*	116.79017	1.61595	275	Salt-lick	2012-03-22	2012-10-19	179
		Small Sepan	*NA*	116.77829	1.58006	263	Salt-lick	2012-05-22	2012-10-21	153
		STA 1	*NA*	116.76877	1.56384	328	Trail	2012-03-21	2012-10-15	209
		STA 2	*NA*	116.77139	1.56097	352	Trail	2012-04-02	2012-10-15	197
		STA 3	*NA*	116.77908	1.55677	369	Trail	2012-03-21	2012-10-15	209
		STA 4	*NA*	116.77110	1.56815	315	Trail	2012-03-21	2012-10-15	209
		STA 5	*NA*	116.75553	1.56789	410	Ridgeline	2012-03-23	2012-10-16	207
		STA 6	*NA*	116.74974	1.55987	433	Old Logging Road	2012-03-23	2012-10-16	208
		STA 7	*NA*	116.75686	1.56583	319	Old Logging Road	2012-03-23	2012-10-16	208
		STA 8	*NA*	116.76578	1.56950	294	Old Logging Road	2012-03-24	2012-10-16	207
		STA 9	*NA*	116.77421	1.56625	316	Old Logging Road	2012-03-24	2012-10-15	206
		STA 10	*NA*	116.78121	1.55177	391	Old Logging Road	2012-03-24	2012-10-15	206
		STA 11	*NA*	116.78563	1.55693	384	Old Logging Road	2012-03-24	2012-10-19	210
		STA 12	*NA*	116.70861	1.53642	181	Old Logging Road	2012-03-25	2012-10-17	207
		STA 13	*NA*	116.71473	1.53772	245	Old Logging Road	2012-03-25	2012-10-17	207
		STA 14	*NA*	116.72564	1.53890	290	Old Logging Road	2012-03-25	2012-10-17	207
		STA 15	*NA*	116.72408	1.54063	284	Old Logging Road	2012-03-25	2012-10-17	207
		STA 16	*NA*	116.73318	1.53952	362	Old Logging Road	2012-03-25	2012-10-17	207
		STA 17	*NA*	116.74249	1.54433	398	Old Logging Road	2012-03-27	2012-10-17	205
		STA 18	*NA*	116.74102	1.54898	465	Old Logging Road	2012-03-27	2012-10-17	205
		STA 19	*NA*	116.73549	1.55637	474	Old Logging Road	2012-03-27	2012-10-17	205
		STA 20	*NA*	116.74165	1.55447	480	Old Logging Road	2012-03-27	2012-10-16	204
		STA 21	*NA*	116.77924	1.58998	376	Old Logging Road	2012-03-28	2012-10-18	205
		STA 22	*NA*	116.78607	1.58269	376	Old Logging Road	2012-03-28	2012-10-18	205
		STA 23	*NA*	116.78786	1.57630	384	Old Logging Road	2012-03-28	2012-10-18	205
		STA 24	*NA*	116.78744	1.56891	397	Old Logging Road	2012-03-28	2012-10-18	205
		STA 25	*NA*	116.78484	1.56341	400	Old Logging Road	2012-03-28	2012-10-18	205
		STA 26	*NA*	116.78365	1.60005	286	Old Logging Road	2012-03-31	2012-10-18	202

		STA 27	*NA*	116.77978	1.59875	289	Old Logging Road	2012-03-31	2012-10-18	202
		STA 28	*NA*	116.77895	1.59501	318	Old Logging Road	2012-03-31	2012-10-18	202
		STA 29	*NA*	116.78093	1.55977	342	Old Logging Road	2012-04-01	2012-10-15	198
		STA 30	*NA*	116.78449	1.56715	409	Old Logging Road	2012-04-01	2012-10-18	201
		STA 31	*NA*	116.76339	1.56753	214	Old Logging Road	2012-04-02	2012-10-16	198
		STA 32	*NA*	116.74682	1.55710	449	Old Logging Road	2012-04-03	2012-10-16	197
		STA 33	*NA*	116.74054	1.54012	419	Old Logging Road	2012-04-03	2012-10-17	198
		STA 34	*NA*	116.71994	1.53928	260	Old Logging Road	2012-04-03	2012-10-17	198
		STA 35	*NA*	116.73759	1.55400	485	Old Logging Road	2012-05-20	2012-10-17	151
		STA 36	*NA*	116.72411	1.53881	281	Old Logging Road	2012-05-20	2012-10-17	151
		STA 37	*NA*	116.73911	1.55117	450	Old Logging Road	2012-05-20	2012-08-14	87
		STA 38	*NA*	116.78517	1.55996	419	Old Logging Road	2012-05-20	2012-08-26	99
		STA 39	*NA*	116.78574	1.55608	391	Old Logging Road	2012-05-21	2012-10-18	150
		STA 40	*NA*	116.78575	1.55608	391	Old Logging Road	2012-05-23	2012-08-25	95
		STA 41	*NA*	116.78857	1.57163	408	Old Logging Road	2012-05-23	2012-07-25	64
2	Logging concession	STA 1	*NA*	116.78864	1.54166	340	New Logging Road	2012-10-22	2014-04-14	540
		STA 2	*NA*	116.79269	1.54134	322	New Logging Road	2012-10-22	2014-04-11	537
		STA 3	*NA*	116.79695	1.53376	230	New Logging Road	2012-10-23	2014-04-16	473
		STA 4	*NA*	116.80007	1.53168	232	New Logging Road	2012-10-23	2014-04-16	507
		STA 5	*NA*	116.79715	1.52262	292	New Logging Road	2012-10-24	2014-04-15	454
		STA 6	*NA*	116.79726	1.52994	289	New Logging Road	2012-10-24	2014-04-15	539
		STA 7	*NA*	116.79426	1.52850	321	New Logging Road	2012-10-24	2014-04-15	418
		STA 8	*NA*	116.79643	1.52637	326	New Logging Road	2012-10-24	2014-04-15	283
		STA 9	*NA*	116.79405	1.52335	281	New Logging Road	2012-10-24	2014-04-15	496
		STA 10	*NA*	116.78828	1.55027	329	New Logging Road	2012-10-19	2014-01-11	429
		STA 11	*NA*	116.79025	1.54675	390	New Logging Road	2012-10-25	2014-04-14	537
		STA 12	*NA*	116.78696	1.54659	381	New Logging Road	2012-10-25	2014-03-07	499
		STA 13	*NA*	116.78568	1.54249	305	New Logging Road	2012-10-25	2014-02-09	473
		STA 14	*NA*	116.79068	1.52864	373	New Logging Road	2012-10-25	2014-04-15	538
		STA 15	*NA*	116.78412	1.53172	235	New Logging Road	2012-11-23	2014-03-20	469
		STA 16	*NA*	116.78571	1.53360	235	New Logging Road	2012-11-24	2014-02-09	443
		STA 17	*NA*	116.78909	1.53609	234	New Logging Road	2012-11-27	2014-04-15	505
		STA 18	*NA*	116.77998	1.53632	235	New Logging Road	2012-12-03	2014-01-14	408
		STA 19	*NA*	116.78740	1.53893	235	New Logging Road	2013-03-27	2014-04-15	385

		STA 20	*NA*	116.78369	1.53963	236	New Logging Road	2013-01-04	2014-04-15	467
		STA 21	*NA*	116.78161	1.52819	235	New Logging Road	2013-01-12	2014-04-14	458
		STA 22	*NA*	116.77776	1.53033	235	New Logging Road	2013-01-15	2014-04-14	455
		STA 23	*NA*	116.78034	1.53128	234	New Logging Road	2013-01-15	2014-04-14	455
		STA 24	*NA*	116.77254	1.52534	235	New Logging Road	2013-01-21	2014-04-14	449
		STA 25	*NA*	116.77474	1.51896	233	New Logging Road	2013-01-21	2014-04-14	449
		STA 26	*NA*	116.77783	1.52013	234	New Logging Road	2013-01-22	2014-04-14	448
		STA 27	*NA*	116.78279	1.52940	317	New Logging Road	2013-03-27	2014-04-14	384
		STA 28	*NA*	116.80275	1.53933	266	New Logging Road	2013-03-30	2014-04-16	383
		STA 29	*NA*	116.80160	1.54426	248	New Logging Road	2013-03-30	2014-04-16	383
		STA 30	*NA*	116.80022	1.54609	254	New Logging Road	2013-03-30	2014-04-16	383
		STA 31	*NA*	116.79839	1.55264	270	New Logging Road	2013-03-30	2014-04-16	383
		STA 32	*NA*	116.79459	1.55590	342	New Logging Road	2013-07-02	2014-04-16	289
		STA 33	*NA*	116.79625	1.55457	335	New Logging Road	2013-03-31	2014-04-16	382
		STA 34	*NA*	116.80244	1.55311	231	New Logging Road	2013-03-31	2014-04-16	382
		STA 35	*NA*	116.79906	1.54093	269	New Logging Road	2013-03-31	2014-04-16	382
		STA 36	*NA*	116.79039	1.55153	352	New Logging Road	2013-06-08	2014-04-14	310
3	Wehea Protected Forest	Butterfly Sepan	1	116.77753	1.58241	263	Salt-lick	2016-05-03	2017-07-24	647
		Small Sepan	2	116.77835	1.58001	263	Salt-lick	2016-05-03	2017-07-24	1288
		Zone 1, primary[c]	3	116.77708	1.57970	314	Ridgeline	2016-05-28	2016-11-07	326
		Zone 1, primary[c]	4	116.77420	1.58061	311	Ridgeline	2016-11-07	2017-07-24	404
		Zone 1, secondary Arb	5	116.77604	1.58058	329	Arboreal	2016-06-15	2016-11-22	320
		Zone 2, primary	6	116.76520	1.57476	366	Ridgeline	2016-05-29	2017-07-24	842
		Zone 2, secondary Arb	7	116.76828	1.57390	322	Arboreal	2016-06-08	2016-10-24	276
		Zone 3, primary	8	116.77748	1.57139	399	Ridgeline	2016-06-10	2017-07-24	757
		Zone 3, secondary Arb	9	116.77240	1.57551	266	Arboreal	2016-06-11	2016-10-24	270
		Zone 3, secondary MR710	10	116.77364	1.56706	256	Active Logging Road	2016-11-12	2017-01-07	112
		Zone 3, secondary RFP	11	116.77036	1.57375	260	Rivine crossing	2016-12-16	2017-03-27	202
		Zone 4, primary	12	116.76196	1.56159	357	Ridgeline	2016-06-07	2017-07-25	823
		Zone 4, secondary Arb	13	116.76435	1.56519	286	Arboreal	2016-06-14	2016-10-19	254
		Zone 4, secondary TT1020	14	116.75837	1.56635	278	Old Logging Road	2016-11-20	2017-05-22	366
		Zone 4[d], secondary TT3000	15	116.74315	1.55624	498	Old Logging Road	2017-03-30	2017-07-25	186
		Zone 4[d], secondary TT3600	16	116.73950	1.55227	505	Old Logging Road	2017-04-03	2017-05-22	98

Zone 4[d], secondary BP	17	116.74083	1.55525	574	Ridgeline	2017-04-03	2017-05-22	78
Zone 5, primary[c]	18	116.78148	1.56186	380	Ridgeline	2016-05-26	2016-10-29	312
Zone 5, primary[c]	19	116.78133	1.56147	366	Ridgeline	2016-10-29	2017-07-24	536
Zone 5, secondary Arb	20	116.77861	1.56167	358	Arboreal	2016-06-09	2016-10-22	270
Zone 6, primary	21	116.77392	1.55750	375	Ridgeline	2016-05-27	2017-07-24	841
Zone 6, secondary Arb	22	116.77814	1.55682	353	Arboreal	2016-06-13	2016-11-23	291
Zone 6, secondary E1520	23	116.77534	1.55678	358	Ridgeline	2016-11-17	2017-01-28	72
Zone 6[d], secondary SG	24	116.77428	1.54553	265	Rivine crossing	2017-02-02	2017-05-21	193
Zone 6[d], secondary KC	25	116.77070	1.55008	358	Ridgeline	2017-02-02	2017-05-21	216
Zone 7, primary[c]	26	116.78264	1.54897	369	Ridgeline	2016-06-14	2016-10-29	274
Zone 7, primary[c]	27	116.78089	1.55026	390	Ridgeline	2016-12-16	2017-03-27	202
Zone 7, secondary Arb	28	116.78475	1.55618	383	Arboreal	2016-06-12	2016-10-28	269
Zone 7, secondary MR2380	29	116.78122	1.55172	392	Active Logging Road	2016-10-29	2017-01-07	140
Zone 7, secondary EO	30	116.78122	1.55686	403	Ridgeline	2017-01-08	2017-03-27	156

[a] Number refers to camera station tag number in Figure 3.S2.

[b] Camera trap day totals that do not add up to the full number of days between the Start and End dates are due to camera trap failures (technical problems, dead batteries, full memory cards, human error, etc) that occurred for some duration between the Start and End dates.

[c] Primary camera trap stations were moved to new ridgeline locations within their same zones part way through this phase due to problems with the original locations.

[d] Station placement was outside the study area adjacent to this zone.

Table 3.S2 A detailed overview of each camera trap record that was assigned to a female identity.

Lumped Scenario ID	Split Scenario ID	Date - Time	Phase	Station	Station Placement	UTM 50N X	UTM 50N Y	Longitude	Latitude
Janet	Candy	2013-03-31 14:06:00	**2**	STA 20	New Logging Road	475939	170177	116.78369	1.53963
Janet	Candy	2013-04-04 07:35:00	**2**	STA 23	New Logging Road	475566	169254	116.78034	1.53128
Janet	Candy	2013-07-18 14:04:00	**2**	STA 25	New Logging Road	474943	167892	116.77474	1.51896
Janet	Candy	2014-02-02 16:37:00	**2**	STA 23	New Logging Road	475566	169254	116.78034	1.53128
Janet	Candy	2014-03-25 16:32:00	**2**	STA 20	New Logging Road	475939	170177	116.78369	1.53963
Janet	Pima	2016-06-11 13:20:00	**3**	Zone 3, primary	Ridgeline	475248	173688	116.77748	1.57139
Janet	Pima	2016-12-28 11:49:00	**3**	Zone 3, primary	Ridgeline	475248	173688	116.77748	1.57139
Penelopi	Auntie	2012-06-01 06:43:00	**1**	STA 8	Old Logging Road	473947	173479	116.76578	1.56950
Penelopi	Auntie	2012-06-02 06:11:00	**1**	STA 8	Old Logging Road	473947	173479	116.76578	1.56950
Penelopi	Auntie	2012-06-09 10:51:00	**1**	STA 8	Old Logging Road	473947	173479	116.76578	1.56950
Penelopi	Isidora	2012-04-26 11:00:00	**1**	STA 19	Old Logging Road	470577	172028	116.73549	1.55637
Penelopi	Isidora	2012-07-10 12:34:00	**1**	STA 18	Old Logging Road	471192	171211	116.74102	1.54898
Penelopi	Pi	2012-07-30 14:45:00	**1**	STA 22	Old Logging Road	476204	174936	116.78607	1.58269
Penelopi	Pi	2017-07-07 10:52:00	**3**	Zone 2, primary	Ridgeline	473882	174060	116.76520	1.57476
Rose	Rose	2013-03-31 10:25:00	**2**	STA 16	New Logging Road	476163	169510	116.78571	1.53360
Rose	Rose	2013-05-13 10:11:00	**2**	STA 31	New Logging Road	477574	171615	116.79839	1.55264
Rose	Rose	2013-06-08 06:27:00	**2**	STA 17	New Logging Road	476539	169786	116.78909	1.53609
Spice	Eva	2012-05-29 08:16:00	**1**	STA 13	Old Logging Road	468268	169967	116.71473	1.53772
Spice	Eva	2012-08-17 12:59:00	**1**	STA 25	Old Logging Road	476067	172805	116.78484	1.56341
Spice	Eva	2012-09-11 06:54:00	**1**	STA 13	Old Logging Road	468268	169967	116.71473	1.53772
Spice	Eva	2012-10-04 06:45:00	**1**	STA 34	Old Logging Road	468847	170139	116.71994	1.53928
Spice	Eva	2014-02-02 13:37:00	**2**	STA 27	New Logging Road	475838	169046	116.78279	1.52940

Spice	Jackie	2012-10-08 13:34:00	**1**	STA 11	Old Logging Road	476155	172089	116.78563	1.55693
Spice	Jackie	2012-11-19 06:35:00	**2**	STA 3	New Logging Road	477414	169528	116.79695	1.53376
Spice	Jackie	2012-12-31 12:21:00	**2**	STA 4	New Logging Road	477761	169298	116.80007	1.53168
Spice	Jackie	2014-01-13 08:25:00	**2**	STA 3	New Logging Road	477414	169528	116.79695	1.53376
Spice	*NA*	2012-06-06 13:49:00	**1**	STA 30	Old Logging Road	476028	173219	116.78449	1.56715
Semma	Semma	2013-08-07 08:23:00	**2**	STA 30	New Logging Road	477777	170891	116.80022	1.54609
Semma	Semma	2013-11-07 05:39:00	**2**	STA 3	New Logging Road	477414	169528	116.79695	1.53376
Semma	Semma	2014-01-08 16:46:00	**2**	STA 3	New Logging Road	477414	169528	116.79695	1.53376
Semma	Semma	2014-02-25 07:46:00	**2**	STA 3	New Logging Road	477414	169528	116.79695	1.53376
Trixie	Barbara	2012-09-16 08:53:00	**1**	STA 14	Old Logging Road	469481	170097	116.72564	1.53890
Trixie	Barbara	2012-10-02 10:16:00	**1**	STA 16	Old Logging Road	470320	170165	116.73318	1.53952
Trixie	Barbara	2012-10-05 10:04:00	**1**	STA 14	Old Logging Road	469481	170097	116.72564	1.53890
Trixie	Barbara	2012-10-09 11:25:00	**1**	STA 13	Old Logging Road	468268	169967	116.71473	1.53772
Trixie	Pansy	2013-01-29 11:47:00	**2**	STA 7	New Logging Road	477114	168947	116.79426	1.52850
Trixie	Pansy	2013-02-06 09:41:00	**2**	STA 7	New Logging Road	477114	168947	116.79426	1.52850
Trixie	Pansy	2013-12-03 06:28:00	**2**	STA 21	New Logging Road	475707	168913	116.78161	1.52819
Trixie	Pansy	2013-12-03 09:42:00	**2**	STA 27	New Logging Road	475838	169046	116.78279	1.52940
Trixie	Pansy	2013-12-18 10:34:00	**2**	STA 21	New Logging Road	475707	168913	116.78161	1.52819
Trixie	Pansy	2013-12-25 11:24:00	**2**	STA 21	New Logging Road	475707	168913	116.78161	1.52819
Trixie	Pansy	2014-01-28 09:57:00	**2**	STA 34	New Logging Road	478024	171667	116.80244	1.55311
Trixie	*NA*	2014-03-05 12:20:00	**2**	STA 27	New Logging Road	475838	169046	116.78279	1.52940

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Thank you to my close friends and confidants. Caroline Schuppli, thank you for being the most dependable, honest, generous friend I could imagine. I am inspired by all that you are. Anna Marzec, thank you for your friendship and camaraderie through this – I am so grateful to have not been on the rollercoaster of these past two years alone. Jess Harding, thank you for always having my back, and loving and supporting me even when I was at my worst. Jan Spilman, thank you for your friendship, insight, and wisdom, which has helped me out of some of my darkest times. Thank you also to Kelly Mannion, Rahel Brügger, Julia Kunz, Kat Koops, Christiaan Conradie, and Ruth Linsky for your friendship. Thank you to Rikka, Gefriel, and Zavea, for being my Indonesian family and home away from home. Thank you to my therapist, for helping me learn to manage my anxiety enough to actually finish this PhD.

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Thank you to Ivan Lenzi, for slogging through this whole thing by my side, for going above and beyond at home and in the field, for supporting me in every way possible, for being the source of balance in my life, and for believing in me even when I didn't believe in myself. The extent of your humour, generosity, honesty, and caring astounds me every day. I feel so privileged to know you and to be known by you, to be your family, and to spend my life with you. And, side note, thank you also for introducing me to cats, and for bringing Empi and Jimmy into our lives.

Thank you to my brother and sister, for being the most hilarious support system and my best lifelong friends. You put up with all of my feelings but keep me in check, you push me but always support me, and you are definitely the coolest kids I ever get to hang out with. I'm so happy to be stuck in the middle of you two. Thank you to my parents; Mom, you taught me organization and attention to detail, and Dad, you instilled in me a love of nature and adventure. Both of you have supported me through everything, and I couldn't have done this without either of you. Thank you for always listening to me, even when all I had were tears, and for always showing up (figuratively, when distance didn't allow for literally) when I needed you. To my whole family, you are the best team a person could ask for, and I am blessed to always have you to come home to.

And finally, thank you to the orangutans for tolerating us (more or less) as we stumbled along behind them, stalking their every move, day after day. And a special thank you to Pi, for letting me in and for making the hardest three years of my life totally worth it. I'm sorry that I cannot protect you anymore. Stay strong, stay safe.

Appendix 1

Terrestrial behavior among wild orangutans (*Pongo pygmaeus morio*) in Wehea Forest, East Kalimantan, Indonesia

Alison M. Ashbury[1], Stephanie Spehar[2], Yaya Rayadin[3,4], Mary Rose C. Posa[5], and Maria van Noordwijk[1]

1. Department of Anthropology, University of Zurich, Zurich, Switzerland; 2. Anthropology Program, University of Wisconsin Oshkosh, Oshkosh, USA; 3. Ecology and Conservation Center for Tropical Studies (ECOSITROP), Indonesia; 4. Biodiversity Conservation Laboratory, Forestry Faculty of Mulawarman University, East Kalimantan, Indonesia; 5. Department of Biological Sciences, National University of Singapore, Singapore

Question

How does habitat type influence Bornean orangutan terrestriality?

How does orangutan terrestriality in the lowland dipterocarp forest of **Wehea** compare to that in the peat swamp forest of **Tuanan**?

Background

- Ground camera trapping studies suggest: [1,2,3]

Heavily disturbed forests and primary undisturbed forests	> **orangutan terrestriality**	Recovering and secondary forests

- Camera traps suggest that orangutans at Wehea are more terrestrial than orangutans at Tuanan:[1,4]
  - Terrestriality at Wehea suggested to be an energy-saving adaptation to a resource-scarce environment[1]
- Direct behavioral data at Tuanan yielded an average of 2.29% of time spent on ground (varies by age-sex class)[4]

Methods

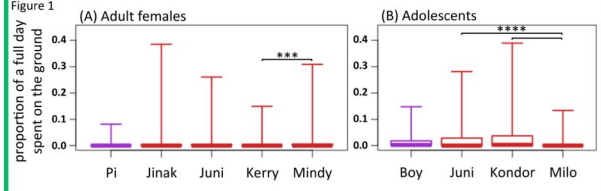
Study Site	Wehea	Tuanan
Location	East Kalimantan	Central Kalimantan
Forest type	Lowland dipterocarp forest	Peat swamp forest
Past disturbance	Until Mid-90s: Selective commercial logging	Early 90s: Selective commercial logging; Until early 2000s: informal logging by local people[5]
Topography and ground	Extremely hilly, varied terrain, ridges and streams; dry ground	Flat; shallow peat, swampy ground
Study period	May 2014 to March 2016	July 2003 to July 2010
Individuals included in analysis, hours of observation	1 adult female and 1 adolescent; 338 hours total	4 adult females and 3 adolescents; 7,888 hours total
Orangutan data collection methods	Nest-to-nest focal follows, instantaneous recording of activity and height in the canopy, all-occurrences recording of notable and rare behaviors[6]	

- **Wehea phenology data collection:** monthly monitoring of 600+ numbered stems, presence of fruit noted; Fruit Availability Index (FAI) = proportion of stems (≥10cm DBH) bearing fruit; FAI divided into categories based on 31 months of phenology data collected between 2011 to 2016 (see Spehar et al. Poster #142), converted to z-scores (following Ref. 7) then divided into 3 categories (Low: $z < -1$; Med: $-1 \leq z \leq 1$; High: $z > 1$)
- **Data analysis:** non-parametric statistics, all performed in R Studio

Results

- **Time on the ground, Wehea:** 0 – 15 % of each day on the ground (2 individuals, n = 46 days, median = 0, mean = 1.3%)
- **Time on the ground, Wehea vs Tuanan:**

Figure 1



Kruskall-Wallis tests for inter-individual variation, ***p<0.001, ****p<0.0001

- **Activities on the ground, Wehea vs Tuanan:**

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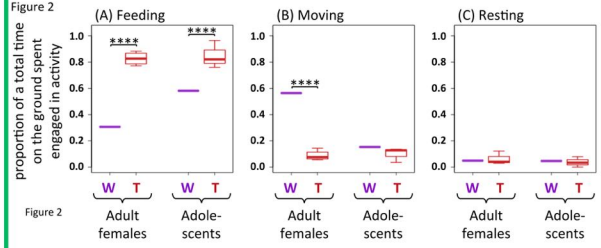

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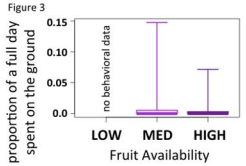

Conclusions

- Overall time spent on the ground did not differ between Wehea and Tuanan
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dry ground at **Wehea**	< **termite-infested rotten logs on the ground**	swampy wet ground at **Tuanan**

- Relative time spent moving on the ground was more at Wehea. This may be related to canopy structure and energy conservation:

Tuanan	• higher tree density • more compliant trees • lower canopy	≈ • easier, energetically less-costly canopy locomotion (tree swaying)[8] • energetically less costly to move up and down between canopy and ground[8]
Wehea	• lower tree density • larger and less compliant trees • higher canopy	≈ • more challenging and energetically costly canopy locomotion • energetically beneficial to maximize distance travelled during ground bouts

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1: Department of Anthropology, University of Zurich, Zurich, Switzerland

2: Anthropology Program, University of Wisconsin-Oshkosh, Oshkosh, WI, USA

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4: Biodiversity Conservation Laboratory, Forestry Faculty of Mulawarman University, Samarinda, Indonesia

5: Department of Biological Sciences, National University of Singapore, Singapore

Poster presentated at the 26th Congress of the International Primatological Society in Chicago, IL, USA, Aug 21-27, 2016

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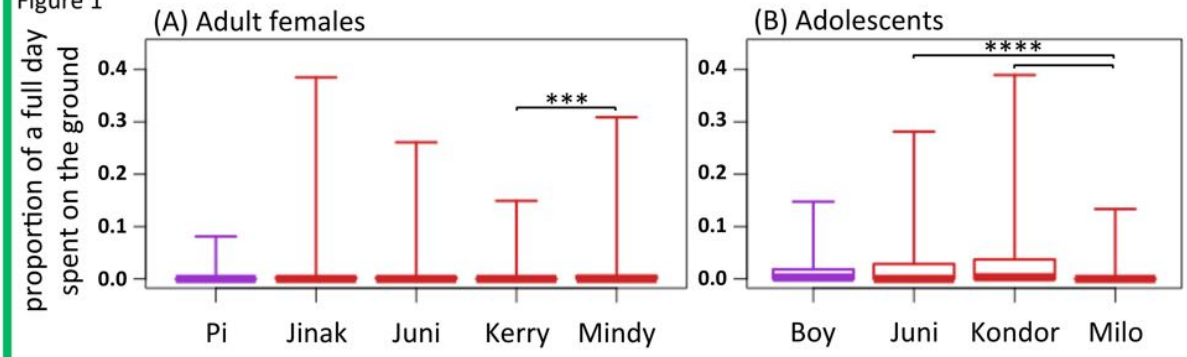

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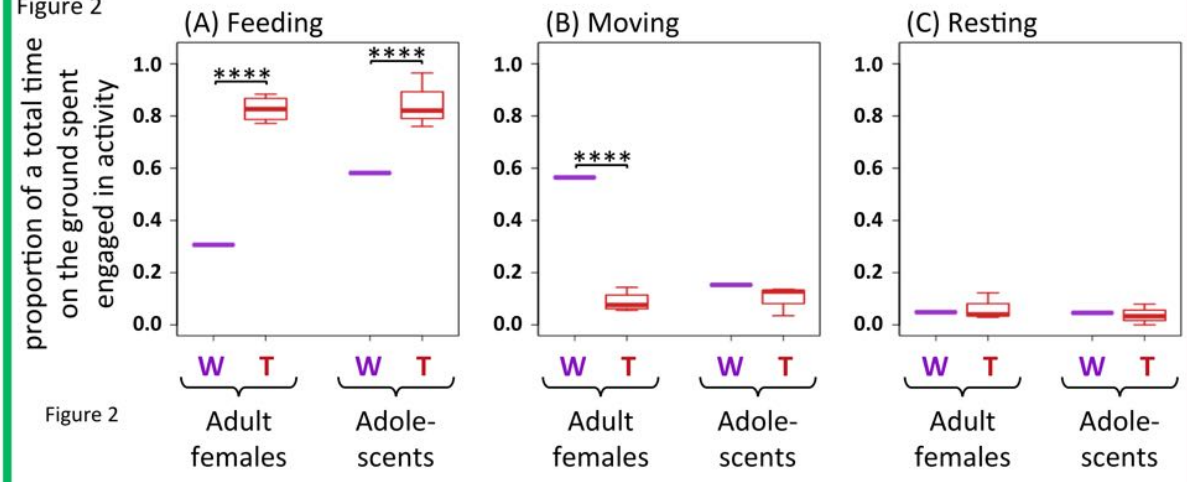

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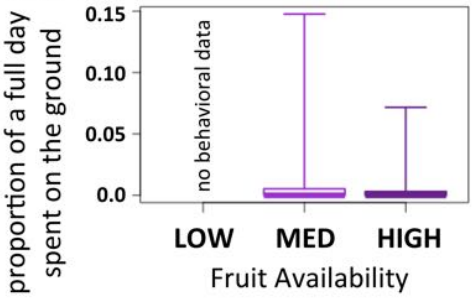

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